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THE ORIGIN AND EVOLUTION OF HYMENOPTERA

INTRODUCTION

Hymenoptera occupy a key position in the organization of living nature, hence in the scientific and practical activities of man. To a certain extent this is due to the taxonomic diversity of this order. Borror, Delong and Triplehorn (1976) assess the number of the described species of Hymenoptera as 108 thousand. This is, however, less than half the total number of their species. Indeed, Brothers (1975) estimates that the aculeate species alone number 70 thousand, and his data on individual groups generally coincide with those of specialists in the relevant fields (12-14 thousand species of ants, Brown and Wilson, 1971; 20 thousand species of bees, Michener, 1974). By 1969 sixteen thousand species had been described in the giant family Ichneumonidae (Townes, 1969), but, as Townes points out, the percentage

* Figures in the right-hand margin indicate the page numbers of the original. Translator.

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of the as yet undescribed species in his vast collection of this group suggests that the total number of their species is close to sixty thousand. In reality this figure is also too low and it is doubtful that the family discussed comprises fewer than hundred thousand species (see more detail in the forward to Heinrich, 1978). The family Braconidae and the superfamily Chalcidoidea can scarcely be much smaller in size than the Ichneumonidae (Noyes, 1978, lists 16.5 thousand described species of Ichneumonidae so that the total number of their species may be over hundred thousand). It would appear that the estimated figure of 300 thousand species in that order suggested by the data in the French Traité de zoologie (Grassé, 1949-1951) is not an exaggeration. This means, however, that in the size of their order the Hymenoptera rank practically next to the beetles, the universally recognized giant of the zoological system (according to Britton, 1970, there have already been described close to 300 thousand beetle species, i.e. more than in any other class or even type, let alone order). Moreover, it should be kept in mind that beetles, similarly to the other major orders of insects (Lepidoptera and Diptera), have been described much more fully than Hymenoptera.

The most important function of Hymenoptera in nature is to stabilize the biocoenoses (continental and predominantly terrestrial ones) by controlling the abundance of other insects. This function is fulfilled by various parasitic (ichneumon flies in the broad sense of the word) and stinging (diverse wasps and ants) higher Hymenoptera. The species capable of a swift numerical response (reproduction) to the quantity of the food resources available, or of a powerful functional reaction (behavioural change) may play here a specific role. We are referring primarily to the rapidly developing Ichneumonidae and ants. This is, however, a complex problem and it has been dealt with in a vast literature on the theory of the population abundance control, as well as on the role of entomophages in biocoenoses. A literature survey and an extensive bibliography pertaining to these problems can be found in G.A. Viktorov's work (1976), as well as in manuals of agricultural

and forest entomology, biological methods of pest control and general ecology.

Without analyzing this problem in detail, it may be noted that in spite of the abundance of entomophages among the most diverse groups of animals (and plants), Hymenoptera occupy a special place among them due to their diversity, to the rapidity and perfection of their reactions, and because of their capacity for specialization. Apart from Hymenoptera, the only group playing a more or less perceptible part in the ecological niche of entomophages are parasitic Diptera. p.4

Another clearly observable, but considerably less important function of Hymenoptera is the consumption of primary products. We should point out here that so far we are referring only to the consumption of vegetative tissues of plants, i.e. to the diet characteristic of a numerically small group (suborder) of the lower Hymenoptera comprising close to five thousand described species (Benson, 1951, 1952). Even though in middle latitudes the lower Hymenoptera (the suborder Symphyta) are comparable in abundance and biomass to Lepidoptera and outstrip them in high latitudes by a considerable margin (Chernov, Rudenskaya, 1975), in relation to the insects as a whole the lower Hymenoptera play a substantial, but not a leading role in the "processing" of primary products.

The pollination of plants involving consumption of pollen and nectar is characteristic of many insects and may be one of the oldest forms of the trophic relationship between the insects and plants (for more details see chapter I). However, some groups of Hymenoptera, first of all the bees, have a special place among the pollinators. The pollen and nectar gathered are used by these insects not only as food for adult individuals, but also for feeding their progeny. The females therefore constantly fly from flower to flower gathering food for their larvae, and thereby ensure a high probability rate of pollinating the plants. The effectiveness of pollination of the plants by bees is particularly high because of their tendency to return to the same plant species. In some cases this is due to their inherent specialization with regard to

plants (in many solitary bees), and in others to the ability of highly specialized species to direct the activities of the foragers towards the most productive source of food during each given period. There has recently been described a third variant characteristic of bumble-bees (Heinrich, 1976) a flexible system of a temporary specialization of individual females.

In keeping with the importance of Hymenoptera in nature's economy, the practical significance of that order for man is also very great. There is no need to dwell on this point, since convincing evidence to that effect can be found in any manual on agricultural or forest entomology, on plant breeding or on the biological method of pest control. We shall merely mention here the possibilities that are opening up for the practical utilization of Hymenoptera in a new direction. The rapid evolution of these insects, combined with their ability to quickly spread and with the specific ecology of their different groups, permits us to use the data from the studies on the geological history of this order in stratigraphy (correlation of deposits), paleoecology and paleobiogeography.

Some of the characteristics of Hymenoptera make them an important model group for solving a number of serious biological problems. For example, the constant haploidy of the males is a link between the Hymenoptera and lower organisms spending most of their life cycle in a haploid state in the sense that they have virtually no hidden recessive mutations (Gershenzon, 1974; see also Rasnitsyn, 1969). This allows us to verify the conclusions regarding the probable role of diploidy in the evolution of the organic world. A paper by Crozier (1977) is devoted especially to the evolutionary genetics of Hymenoptera.

The origin of sociality is an even more important problem and it is solved primarily on the basis of the evidence pertaining to Hymenoptera. This problem is dealt with in a large number of publications, some of which we cite further on (part III, chapter 4).

It is common knowledge that the studies on Hymenoptera have greatly contributed to our understanding of animal behaviour. We are referring in particular to the classical works by Fabre

(1879-1907), Baerends (1941), Frisch (1955) and Malyshev (1959, 1966), as well as to those of many other authors (see the surveys by Tinbergen*, 1969; Shoven*, 1972; Khaind*, 1975).

The objective of this work is to trace, preferably simultaneously in the paleontological and recent materials, the evolution of the order on the level of the superfamily and, wherever it is possible, of the family. The processes occurring on a lower taxonomic level (e.g. different aspects of the evolution of behaviour or modes of the morphological evolution) will not be specially examined even if they have a general significance. p.5

This work sums up our previous studies on the lower Hymenoptera and is a continuation of that research (Rasnitsyn, 1969). Since, however, the object of investigation has now been expanded to encompass the order as a whole, the character of the work has altered considerably. First of all we are compelled to dispense with the special morphological outline: given the detailed nature of that outline in the previous work, it would have taken here too much space, and with a lesser amount of detail it would be useless. We were also forced to eliminate the detailed discussion of theoretical problems and descriptions of the fossil material. A significant portion of the descriptions of Mesozoic Hymenoptera has been published by the author in his other works (Rasnitsyn, 1963, 1964, 1965b, 1968b, 1969, 1972a, 1973, 1975a, 1977b and c; Kozlov and Rasnitsyn, 1979); the descriptions borrowed from other authors are quoted in the papers listed above and in respective chapters of this work.

We felt that, in spite of its limitations, the objective specified was currently of interest for two reasons. The author began a systematic study of fossil Hymenoptera from the collections of the Paleontological Institute of the USSR Academy of Sciences in 1961. Even though by that time there had been described

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* Transliteration. Translator.

(taking into account the subsequent taxonomic revisions) a mere 22 species of Mesozoic Hymenoptera belonging to 12 families, the material accumulated testified to a great diversity and specific character of the Mesozoic fauna. The recent fauna of that order, considered on the level of the superfamily or even family, formed in the Mesozoic, and studies of Mesozoic fossils therefore promised to yield important data for understanding the evolution of the order. To what extent that objective has been met, will be seen from the further account. We shall merely mention here that by the beginning of 1977 the number of the Mesozoic Hymenoptera described was 226 species representing 45 families.

The paleontological investigations were not regarded as the end in itself, but as a method, primarily as one of the methods of studying the evolution of Hymenoptera. Many works in that field had already been published and continued to appear in print after 1960. Most of these works dealt, however, only with a portion of the order, commonly a small one (isolated families, less often superfamilies, and only in rare instances taxa of a higher rank). The last relatively detailed work pertaining to the order in its entirety dates back to 1919 (Börner, 1919). The work by Königsmann (1976-1977) should also cover the Hymenoptera as a whole. I am not referring to this kind of works the well-known monographs by S.I. Malyshev (1959,1966), since this author focuses only on the evolution of behaviour in Hymenoptera and ignores completely morphological data, which accounts for many of the obvious errors in his constructions (Viktorov, 1959; Tobias, 1975a). Behavioural characteristics are, of course, no less important in phylogenetic reconstruction than morphology, but so far they have been considerably less well studied than morphology and lag far behind the latter with regard to the number of the attributes accessible for analysis, information available on different groups of the order, and data on the reliability of different characteristics as material for evolutionary constructions (so far as we know little of the extent to which different behavioural characteristics are subject to parallel development in various groups). Therefore phylogenetic

reconstructions based exclusively on attributes of behaviour cannot be regarded as well substantiated, at least in the case discussed.

Various researchers focused considerable attention on fundamental problems, such as the origin of Hymenoptera as a whole and of the higher Hymenoptera in particular (Handlirsch, 1906-1908; Tillyard, 1924; Martynov, 1937a; Ross, 1937; Crampton, 1938, Chen, 1946; Bradley, 1956; Viktorov, 1959; Malyshev, 1959, 1966; Martynov, 1959; Tobias, 1975a). There has been advanced a large number of hypotheses, some of which may be close to truth, but lacking a solid paleontological basis, remain largely speculative. p.6

These were the circumstances which prompted us to formulate the composite objective: to work out a comprehensive, though perhaps not too detailed, picture of the origin, phylogenesis and systematics of Hymenoptera by using the paleontological, morphological and ethological data available to the fullest possible extent. Prior to proceeding with the exposition of the results obtained, we wish to explain the reasons for some of our decisions, on the subject of which we anticipate the harshest criticism. We are referring to some of the aspects of our theoretical platform, i.e. the system of beliefs which determined the course of our investigations.

The most important problems are those of the relationship between the phylogenesis and the systematics, and the methods of constructing a system. These problems were already discussed earlier (Ponomarenko, Rasnitsyn, 1971), but some of the theories formulated in that work should be reiterated here once again.

There have been advanced three possible solutions to the problem discussed. Two of them ignore either the relationship between the taxa (phenetics) or the scale of differences between the taxa (cladism), while the third one (phylogenetic systematics designated by the cladists as typological) attempts to take into account both these factors. A taxon in the definition of the cladists includes all the descendants (but only the descendants) of a given ancestor, regardless of the magnitude of differences between them; moreover, each divergence gives rise to new taxa. A taxon in the

definition of the pheneticists is a continuum: its members may be arranged in a continuous chain, either simple or branching, in such a manner that the taxonomic distance between any two successive members of the taxon in that chain is invariably smaller than the distance between any members of this and other taxa. A taxon of the phylogenetic system is a monophyletic continuum differing from the one described above in that the continuum must include the closest common ancestor (commonly a hypothetical one) of all the members of the given taxon. Monophylesis is interpreted in a broad sense and includes paraphylesis, i.e. instances where a taxon meets our definition of monophylesis, but is ancestral to another taxon of the same or of a higher rank (the nearest common ancestor of all the members of the taxon may be the ancestor of forms other than its members).

From the viewpoint of the author the ultimate objective of the systematics is to build a system which would reflect best of all the averaged balance of similarities and differences in all the possible attributes (including those that have not been studied as yet) and would therefore have the greatest prognostic capability. It means that this system can accommodate new characteristics and new taxa more readily than any other system and is therefore subject to less frequent changes. The system is envisaged here as the optimal interdisciplinary language in biology, a system of concepts that are as comprehensive as possible (each name in the designation of a taxon should be based on a conjunction of attributes and features that are important to evolutionists, physiologists, geneticists, agronomists, etc.).

It would appear that the ideal system could be built most effectively with the help of phenetic methods that aim precisely at achieving a balance of similarities and differences. However, these methods take into account only a definite assortment of the already known characteristics, and their prognostic capabilities are rather limited. The phenetic approach is fully compatible with polyphylesis of the taxa, but, as is well known, the discovery of polyphylesis and more thorough subsequent study of the polyphyletic group almost invariably reveals its artificiality, the depth of the previously unnoticed differences between

the monophyletic subgroups of the polyphyletic taxon.

In this case it is particularly clearly evident how phylogeny predicts the features of the system which cannot be detected by phenetic methods in the present state of our knowledge.

Unlike the phenetic systematics, the phylogenetic approach rests on the phylogenesis, but is merely an effective method of constructing a system, a method allowing us to predict many of its important features, rather than the ultimate goal (the ideal which must be reflected in the system). p.7

In contrast to these two trends, cladism takes into account only the phylogenesis or, more precisely, the genealogy. According to this concept, each divergence gives rise to two new taxa ("sister groups"), while the ancestral group disappears. All the offspring of the two "sister groups" remain members of their respective taxon, and each new divergence yields two new taxa of a progressively lower rank.

The postulates of cladism lead to practically unacceptable results. First of all this trend advances us towards the ultimate goal of systematics, as it was formulated earlier, in the measure to which the evolution is uniform and divergent, and in our experience that measure is rather small. Indeed, given a uniformly divergent evolution, the multicellular descendants of some sort of Flagellata could not become a group differing more markedly from its nearest relatives than the latter do from the other flagellates. Under real conditions cladism takes us away from our objective rather than leads us to it, unless we regard a simple description of genealogy as the purpose of the system.

Cladism also has other shortcomings of a more particular nature, one of which (the impossiblity of recognizing the ancestors existing in reality) became clearly apparent when Konigsmann (1976) attempted to apply this concept to Hymenoptera. The conjunction of the known facts indicates with certainty that all the Hymenoptera originated from the family Xyelidae (Rasnitysn,

1968b, 1969). In that case cladism dictates that the whole order must be included into Xyllidae (and practically all of it into the subfamily Madygellinae). This solution is obviously unacceptable, but Konigsmann easily overcomes the difficulty. Xyelidae have distinctive heteronomous antennae of a more advanced appearance (apomorphic) than the antennae found in most of the recent Hymenoptera, but a special analysis has shown that even the structure of the antennae corroborates the ancestral nature of Xyelidae (Rasnitsyn, 1968b,1969). Konigsmann is well aware of all this, but, without entering into discussion, he simply declares that insects with antennae of the kind found in Xyelidae could not have been ancestors of all the Hymenoptera.

Cladism thus appears to be a sterile trend in systematics in spite of its surprising popularity. This does not detract, however, from our high rating (Rasnitsyn, 1969; Ponomarenko, Rasnitsyn, 1971) of the method of phylogenetic analysis developed by the cladists (Hennig, 1953, 1965).

The phenetic trend appears to be less promising or less independent than the phylogenetic trend. In future its methods of the quantitative assessment of similarities (taxometric methods) may prove to be an important tool of phylogenetic systematics (Ponomarenko, Rasnitsyn, 1971) in spite of their present shortcomings. Different taxometric techniques applied to the same material yield different results that are generally no better than the results obtained by traditional methods of intuitive systematics (we are referring to the ways of evaluating various characteristics and of assessing their relative importance: the intuitive way in traditional systematics and the formalized way in taxometry). Moreover, the advantages and shortcomings of different methods and the limits within which they can be applied are somewhat obscure, as a result of which the choice of the method introduces a large dose of subjectivity into the investigations cancelling out the advantages of the quantitative analysis. At this time the most urgent task may be to analyze the properties and areas of application of taxometric methods rather than their use for developing a system (Rasnitsyn, 1972b).

The attitude to taxometric methods is reflected to a certain degree in solution of specific problems pertaining to the taxonomic rank of different groups. One of the most important problems of systematics is to ensure that taxa of the same rank be comparable with regard to the magnitude of their dissimilarities, diversity and size. Theoretically taxometry appears to be the optimal method for solving this problem. Attempts at using it have also been made with reference to Hymenoptera, including those by the author of this work (Rasnitsyn, 1972b), but, as was mentioned earlier, we found no obvious or consistent advantages in taxometry versus the traditional intuitive methods. Another p.8
attempt was made by Brothers (1975) in his classical work on systematics and evolution of the aculeate Hymenoptera. Taxometric methods are used not only in the phenetic, but also in the plylogenetic systematics, and Brothers employes precisely the latter variant calculating the taxonomic distance along the branches of the plylogenetic tree. The criterion for estimating that distance is the number of evolutionary steps in the given interval (the number of apomorphic, i.e. advanced characteristics acquired within that interval). That number is assessed with regard to the spread of the characteristics (their susceptibility to parallel development) and size of the group, the ancestor of which is at the top of the segment measured. The assessment lowers the rank of small segregated groups and reduces the number of small (in size) taxa of a high rank.

The choice of the method is here largely subjective, as is always the case in taxometry. The advantages of the measurements taken along the branches of the tree are not obvious: first of all, taxometry, being rigidly tied to phylogeny, ceases to be an independent index capable of controlling our phylogenetic hypotheses to any extent; secondly, in the event of the apormorphic changes within each segment being few, the calculations would yield highly unstable results markedly dependent on the assessment of the extent to which each particular characteristic appears to be apomorphic. Furthermore, it may be justifiable to evaluate the characteristics by their tendency to arise independently in phenetic

taxometry, where an increase in the number of the attributes reliably denoting kinship is essential for constructing a good system. In this case, however, the plylogenesis is known and the only factor measured is the magnitude of the changes occurring at each given evolutionary stage. The reliability of the character is here therefore immaterial for reconstructing the phylogeny. We only have indirect evidence that it is more difficult to arise for an attribute occurring rarely and that this attribute therefore should have a greater effect on the taxonomic distance. The nature of the dependence between the rarity of the given attribute and its effect on the taxonomic distance, i.e. the form in which the frequency of occurrence of that characteristic should be included into the equation of the distance, is, however, obscure. It is equally unclear whether there is any point in taking into account this index alone, while ignoring the others which do not lend themselves readily to a quantitative assessment, but are equally important a priori (e.g. the magnitude of the changes occurring only once). The same may be said concerning the assessment by the size of the group: what are the theoretical criteria for lowering artifically the rank of the groups with a limited number of species, and why did Brothers introduce into the formula the number of the species to the power of 1/3 rather than to something else?

Questions of this kind also arise with regard to all the other taxometric methods, and so far none of these methods offers definite advantages versus the traditional methods of intuitive systematics. Consequently these are the methods that should be used to ensure the comparability of taxa of the same rank. But if we rely on individual experience and intuition, the responsibility for "equalizing" the ranks lies primarily with the specialists dealing in their research with the system of respective large groups of organisms as a whole. It is not accidental that according to the rules of ethics in systematics a researcher may change the rank of subordinate taxa from the group in which he is specialized, but not the rank of the group itself.

These are precisely the considerations which encouraged the author to change the rank of many taxa among the Hymenoptera (mainly taxa at the level of a family). We cannot claim to have achieved a subjective feeling of having made the taxa comparable, but there are reasons for this. Indeed, the interpretation of the rank of the taxa at the group level of a family varies widely in Hymenoptera. Moreover, in most instances the ranks are lower than the average standard of a family among the insects and only in some cases does the system appear to be "overdifferentiated" (the modern systems of the superfamily Chalcidoidea, the systems including several families of bees and digging wasps). The most logical solution under the circumstances would be to reduce the family unit among the Hymenoptera so that it would fit the general entomological standard of a family, but it appears to be impossible: the largest and most diversified hymenopterous families Ichneumonidae and Braconidae do not lend themselves to differentiation at the present time. On the other hand it would be unwise to bring all the families to the level of these two, since it would lower the rank of practically all the superfamilies to the level of families and would result in many of them in an acute deficite of the ranks intermediate between the family and the genus. p.9

The two other questions which should be elucidated here in addition to our attitude to cladism and our reasons for revising the taxonomic rank of some groups are: a) the use of the term "parallelism", and b) the age of the given group, i.e. the time when it came into being relative to its initial appearance in the paleontological record.

Without examining the problem of parallelism in depth (see Tatarinov, 1976, for a more detailed analysis of this problem), we wish to note the following. Parallelism is commonly used in conjunction with the concepts of divergence and convergence, but the only unambiguous concept of the three is divergence, while the two others are less well defined. Some authors interpret parallelism as the acquisition of similarity by closely related forms, and convergence as a similarity occurring secondarily in distantly related organisms on the basis of a different organization.

Other researchers refer to convergence the instances when the similarity between two groups increases in the process of the evolution, and regard the instances where the similarity remains strictly constant, as parallelism, which thus becomes a border case between convergence and divergence. Both approaches are frought with considerable difficulties. The former fails to clarify what level of taxonomic distance is sufficient for a concrete case to be regarded as convergence. Furthermore, the very fact of its being a convergence in that sense is not obvious. Different classes of Chordata are, for example, rather distant groups, but at least one of their clearly defined adaptations occurring independently is due to the fundamental unity of organization of the type. We are referring to their fishlike body shape and the corresponding mode of swimming, which can generally be achieved only in the presence of a resilient internal body axis (a chorda or a vertical column) accumulating the energy of oscillatory movements. At the same time this axis is a character inherited by Chordata from a common ancestor, a direct reflection of their genetic relationship.

The effectiveness of the second approach to the problem is doubtful for two reasons. First of all, divergence, parallelism and convergence in isolated characteristics are trivial, and ascertainment of their existence contributes little to our understanding of the evolution. If, however, we are concerned with the taxonomic level (the direction of changes in the aggregate balance of similarities and differences), then to identify these phenomena we must have precise and objective methods for assessing the taxonomic similarity. However, as was mentioned earlier, no such methods have been developed as yet and so far it is impossible to establish parallelism with confidence. Secondly, the very existence of convergence interpreted as an increase in the taxonomic similarity in the course of the evolution, has not been proven so far. At least the author is unaware of any attempts to prove the existence of such factors, not even with the help of one of the known methods of taxometry.

The first interpretation of the concepts of convergence and parallelism thus appears to be inoperative, and the second interpretation remains valid as the problem of the existence of convergence on the taxonomic level, but the notion of parallelism appears there to be practically meaningless. It therefore seems to be advisable to retain the term "parallelism" with reference to the phenomenon of two (or several) groups evolving in the same or similar direction, as in the case of their developing similar adaptations regardless of whether their taxonomic similarity remains constant, increases slightly or diminishes. This is the sense in which A.S. Serebrovskii (1973) interprets parallelism and in which this term is used in our work.

The last problem concerns the time interval between the occurrence of a taxon and its appearance in the paleontological record. For groups of a high taxonomic rank (on the level of a family or higher) differing markedly from their closest relatives, this interval is commonly believed to be of a considerable duration, of the order of a geological epoch, period or even several periods. One of the extreme positions is that of A.L. Takhtadzhyan (1970), p.10 who places the appearance of angiosperms in the Triassic or even Permian, even though their first reliable finds are known only from the Cretaceous period (Vakhrameev, 1973; Krasilov, 1975; Hughes, 1976). In many instances the great length of the unknown period in the existence of a taxon is beyond doubt (wherever the ancestral taxon has been found in a fossil state in deposits that are younger than those hosting its descendents) and the delay may find a natural explanation in taphonomic (para-ecological) factors (i.e. conditions of burial of the given group). For example, the first primitively apterous insects, ancestors of winged forms (bristle-tails in the broad sense), have been found only in the Middle Carboniferous, whereas winged insects themselves are known since the Lower Carboniferous. The late appearance of bristle-tails in the record is due to their predominantly edaphic (in the broad sense) mode of existence with little chance of fossilization, and it is not accidental that in the Paleozoic there have been found only distinctive bristle-tails that lived

near bodies of water or may even have been amphibian (Monura), while more typical groups appear for the first time in the form of inclusions in Late Cretaceous fossil resins (as for the "bristle-tails" described by Sharov in 1948, they are probably larvae of Ephemeroptera). Another example of the unknown (hidden) period in the existence of a group is the appearance of parasitic Hymenoptera of the family Diapriidae later (in the Late Cretaceous) than that of their descendants Serphitidae and Scelionidae (the early and latter half of the Early Cretaceous, respectively). In this case it may be due to the small size of the insects with which we are dealing, since small insects rarely leave impressions in sedimentary rocks. They are found more frequently in fossil resins, but the Early Cretaceous Hymenoptera are known precisely from impressions. Finds of Early Cretaceous Serphitidae and Scelionidae are but a few (a remain per family) and the lack of finds of Diapriidae synchroneous with them may be purely accidental. We can even do without this assumption. Scelionidae and Serphitidae develop as egg parasites and, judging from Scelionidae, have a relatively large assortment of hosts (the hosts of Serphitidae are unknown). Diapriidae were initially parasites of higher Diptera (Muscomorpha) that were still very rare during the Cretaceous period (Zherikhin, 1978). It is entirely probable that Diapriidae, which appeared earlier than either Scelionidae or Serphitidae, were for a long time few in numbers and their chances of being preserved in burials were low. The two other groups changed their feeding habits and hosts and rapidly flourished, probably already in the Early Cretaceous times (their extraordinary abundance in the Late Cretaceous is beyond doubt), and remains of these groups have been found even in uncharacteristic types of burials (sedimentary rocks).

In some cases the lengthy unknown period of existence turns out to be an artefact resulting from the difficulties of interpreting relationships. This happens, for example, if the law of the irreversibility of evolution is interpreted too literally. In particular, the most ancient (Triassic) Hymenoptera are represented

only by the family Xyelidae. This family had been regarded until recently as an obviously blind (dead-end) branch of the lower Hymenoptera specialized on a very archaic basis (Ross, 1937; Benson, 1038; Richards, 1956). Ancestors of the bulk of Hymenoptera remained unknown. It was, however, subsequently demonstrated that the apomorphic characteristics of Xyelidae (heteronomous antennae, see above) do not preclude the derivation of all the other Hymenoptera from that family, but, on the contrary, evidence a genetic continuity in that line (Rasnitsyn, 1968b, 1969). The hypothesis regarding the alleged ancestors of Hymenoptera that are not represented in the paleontological record because of the hidden nature of their existence, thus proved to be superfluous.

The generally accepted belief in the universality of the unknown period of evolution is based primarily on the faulty extrapolation of analogous facts and hypotheses testifying to a later appearance or even total absence of one or another group from the paleontological record and, secondly, on the extrapolation of the observed rates of evolution for the period of occurrence of taxa of high ranks. There are, however, well-argumented hypotheses directed against such extrapolations (the hypothesis p.11
of quantum evolution, Simpson, 1948), as well as data evidencing that the observed rates of evolution are, as a rule, very low relative to its potential rates determined by the intensity of the flow of genetic diversity through the evolving totality (Rasnitsyn, 1971b; Rodendorf, Zherkhin, 1974). All this compels us to reject the generally accepted notions concerning the duration of the hidden (unknown) period of evolution. In this work the time when a group arose is assumed to be significantly different from the momemt of its appearance in the paleontological record only in the cases, where the hypothesis to the contrary is obviously wrong.

In conclusion we wish to take this opportunity to express our profound appreciation to the collective of the Arthropoda Laboratory of the AN SSSR* Paleontological Institute and to its

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* AN SSSR=USSR Academy of Sciences. Translator

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PART I

THE POSITION OF HYMENOPTERA IN THE SYSTEM OF INSECTS

Chapter 1

The origin of winged insects (Pterygota)*.

It is highly probable that insects originated not from polypods (including the orders Protura, Diplura and Colembola), but from more primitive aquatic Arthropoda that may have been close to some extent to Myriopods. The time when insects came into being remains unknown. Initially insects may have inhabited relatively large crevices in the substratum of the kind of fissures in the cliffs, cavities underneath the rocks, ground cover, windfallen trees, etc., and prior to that in the ejects of ancient seas cast on the shore. Primitive wingless insects are differentiated into two orders: Thysanura s.str. (=Zygentoma) and Archaeognatha (including Monura that are almost identical in morphology to the early larvae of Archaeognatha, figs 1-3, and may be a neotenic group).

Thysanura s.str. could hardly have been the ancestors of winged insects (subclass Pterygota), which probably arose from the common ancestor of both orders or even from insects that are closer to Archaeognatha. The wings of Pterygota may have evolved directly from the paranotum, i.e. the free margin at the boundary of the dorsal and pleural body walls (which does not rule out the participation of pleural tissues in their formation, as is maintained by Bocharova-Messner, 1968).

A fairly orderly and consistent scheme of the ecological and morphological evolution of insects during the period of the development of flight can be built if we assume that the ancestors

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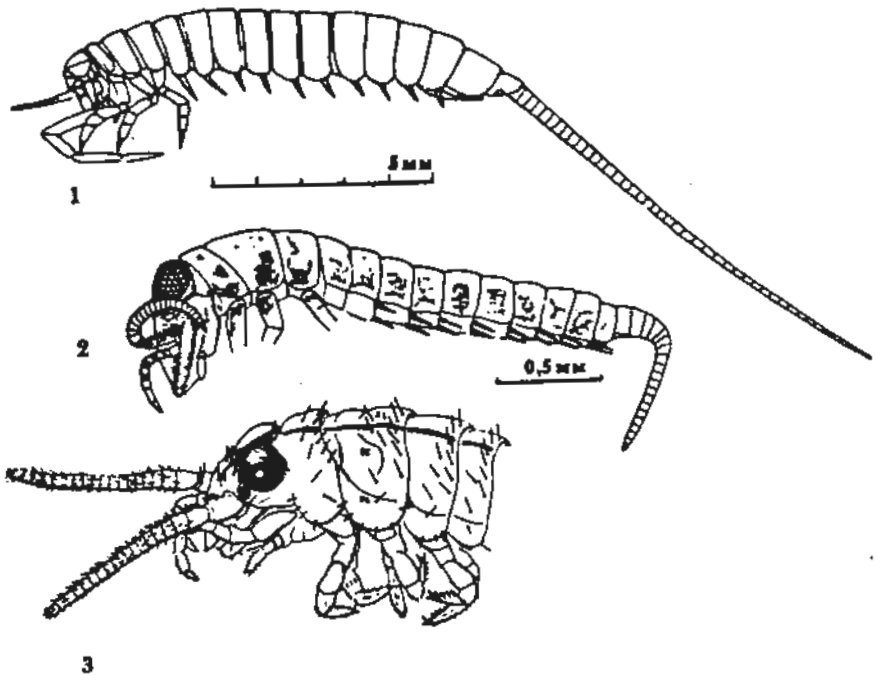
* The views of the author on this problem are outlined in a special work (Tasnitsyn, 1976); they are presented here in a concise form and with the barest minimum of supporting evidence.

of Pterygota (fig. 4) lived in plants (including trees) and fed on their generative organs. Flight was preceded by the "jump-fall" type of locomotion that was used for a variety of purposes. First of all it allowed the insects to escape when attacked by predators, such as Chelicerata or Polypodiaceae, which may have preyed not only above ground, but also in trees. Its second use was particularly important. Hopping from branch to branch enabled the insects to intensify considerably their feeding process, since it eliminated idle runs from the terminal sporangia of one branch along the trunk or stem to the sporangia at the tip of another branch. At the same time it reduced the probability of encountering predators.

The use of the "jump-fall" placed in an advantageous position the individuals capable of maintaining a correct orientation of their body in the air (particularly when hopping from branch to branch, where it is essential to take hold on the substratum right away), and of gliding as far as possible in the desired direction. Expansion of the paranota met both these requirements. Moreover, the advantage gained from the increase in the size of the stabilizing and carrying planes was greater in large insects.

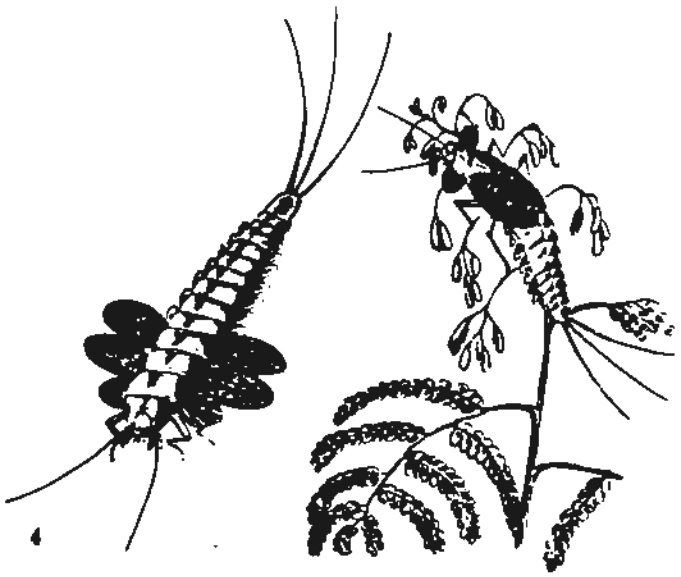
The posterior end of the body in the ancestors of Pterygota was probably sustained in the air by caudal setae (anal filaments). It may therefore have been mainly the anterior paranota that were subject to expansion, particularly those of the heavier thoracic segments. Simple expansion of paranota could not have been particularly great: laterally projecting processes impede locomotion over uneven substratums, such as tree trunks, branches and leaves, or, particularly, the ground surface. Modification of the shape of the paranota would be only partly effective, and the only possible radical solution to this problem may have been the abjunction of the paranota and development of the ability to fold them back in the state of rest and to spread them p.13 in the air. As is well known, the abjunction of cuticular processes and especially of the lateral lobes of tergites is not a particularly rare phenomenon in Arthropoda.

Fig. 1-3



Juvenile and juvenilized Archaeognatha
1-Dasyleptus brongniarti Shar.; Upper Permian from the Kuznets basin; 2-Larva of the Machilidae gen. sp.; recent; 3-Larva of Dita hibernica (Carp.), recent (1-after Sharov, 1957, with some changes; 2-from Bitsch, 1964; 3-from Bartlet, 1949).

Fig. 4.



Hypothetical ancestors of winged insects (reconstruction by A.G. Ponomarenko; from Rasnitsyn, 1976).

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From the mechanical viewpoint the mobility of the horizontal lateral processes (paranota) can be achieved more readily in the vertical (the flapping movements) than in the horizontal plane (folding and straightening out of the paranota) and may have preceded the latter historically. Sharov believes (1973) that the presence of a deep furrow at the base of the wing cases in some of Palaeodictyoptera (table 1, fig. 1) testifies to the vertical mobility of the nymphal wing. The nymphs of the Carboniferous Protoblattodea had a similar wing structure (table 1, fig. 4). Nymphal wings of this kind with a broad base and with the tips oriented obliquely backwards may correspond to the early developmental stage of the precurser of wings and may testify to the extreme antiquity of their vertical movements. It is unlikely that the function of these movements was active flight; in all probability it was rather the orientation of the body during the jump. p.14

The next stage in the prehistory of the wing may be reflected by the older nymphs of some of Palaeodictyoptera, in particular of Tchirkovaea M.Zal. (Sinichenkova, 1979). Alary rudiments were very large in the nymphs of Tchirkovaea M.Zal.; in late nymphs they measured up to one-third of the length of the imaginal wing and even in relatively young nymphs the length of each rudiment was several times greater than the width of the thorax. Wherever the elytron has been preserved together with half the tergite torn along the molting suture, it is oriented almost straight out laterally, particularly in the later stages (plate 1, figs 2-3). If this was its permanent position, it would be difficult to visualize an environment in which an insect of that kind could exist. The wing cases could probably be folded backwards when in repose. This is evident from their narrow and relatively weakly sclerotized base with a well-developed axillary apparatus. Herdina mirificus Carpenter et Richardson is another form that may be used as a model of insects at one of the last developmental stages preceding the appearance of flapping flight (table II, fig. 5).

It is highly significant that, when folded, the primitive wings in the ancestors of Pterygota were appressed to the cylindrical body, hence had an oblique position with the lowered anterior edge and raised posterior edge. This position is similar to the roof-like folding of the wings that may have arisen precisely as a result of their subsequent expansion and joining of their posterior edges.

It is therefore assumed that even the first true Pterygota were capable of folding their wings in repose. The hypothesis of Handlirsch (1906-1908) and Martynov (1925) maintaining that the primitive wings were spread out and did not fold (Martynov makes this claim only with regard to Palaeoptera), is unacceptable for two reasons. First of all spread-out wings impede free locomotion over the substratum and are possible only in insects capable of fairly perfect flight, which we cannot expect from the original Pterygona. Secondly, we know many instances where insects lost the ability to fold wings that was characteristic

of their ancestors (many Lepidoptera and Diptera, some Hymenoptera), but there appear to be no reliable cases of the reverse phenomenon on record (i.e. transition from permanently spread-out wings to wings folding in a roof-like or flat manner underneath the abdomen). Furthermore, the structure of nymphal wings in Tchirkovaea testifying to their ability to move in the horizontal plane, also evidences that the permanently spread-out position of the wings in Palaeodictyoptera is a secondary development.

In support of her hypothesis regarding the secondary nature of folded wings in Diaphanopterodea (a Paleozoic order of Palaeoptera) Kukalova points out (Kukalova-Peck, 1974) that the axillar plates of their wings are fused similarly to those of other Palaeoptera. It should, however, be kept in mind that the disposition of the axillar plates and the manner in which they are connected are highly variable in Pterygota except for the axillar sclerites as such, the first and second ones in particular. The shape, position and mode of junction of the basivenalia (i.e. plates located more distally than the axillar plates) may vary markedly within individual orders or even families, as is evident even from Kukalova's data; they may, indeed, be different in the anterior and posterior wings of the same insect. Moreover, the reduction of the basivenalia and their fusion with one another and with the axillar plates may be much deeper in insects that are capable of folding their wings than in the forms devoid of that faculty. p.15

In many instances we may in fact be dealing not with the fusion of individual plates, but, on the contrary, with the differentiation of the initially weakly subdivided sclerotized region at the base of the wing. The structure of the basal parts of the wing in Diaphanopterodea therefore probably should not be used as evidence of the secondary nature of their ability to fold wings.

An additional argument in support of the primary nature of the roof-like mode of folding the wings is as follows. In addition to the roof-like folding, there are also the flat and the streamlined appressed modes of folding, where instead of meeting in the saggital plane, the wings overlap to varying degrees. In contrast to the flat folding, in the event of the wings overlapping one another the anterior divisions of the wings /in repose/are downfolded/covering partly the sides of the insect. The two latter modes of folding provide for a more compact position of the wings at rest than does the roof-like pattern, and should be regarded as more advanced than the latter. The change from one of these modes to the roof-like folding is therefore improbable. To our knowledge there are no reliable examples of that kind, as /changeover of the/ there is no record of the/wings spread out in the state of rest to the wings folded on the abdomen.

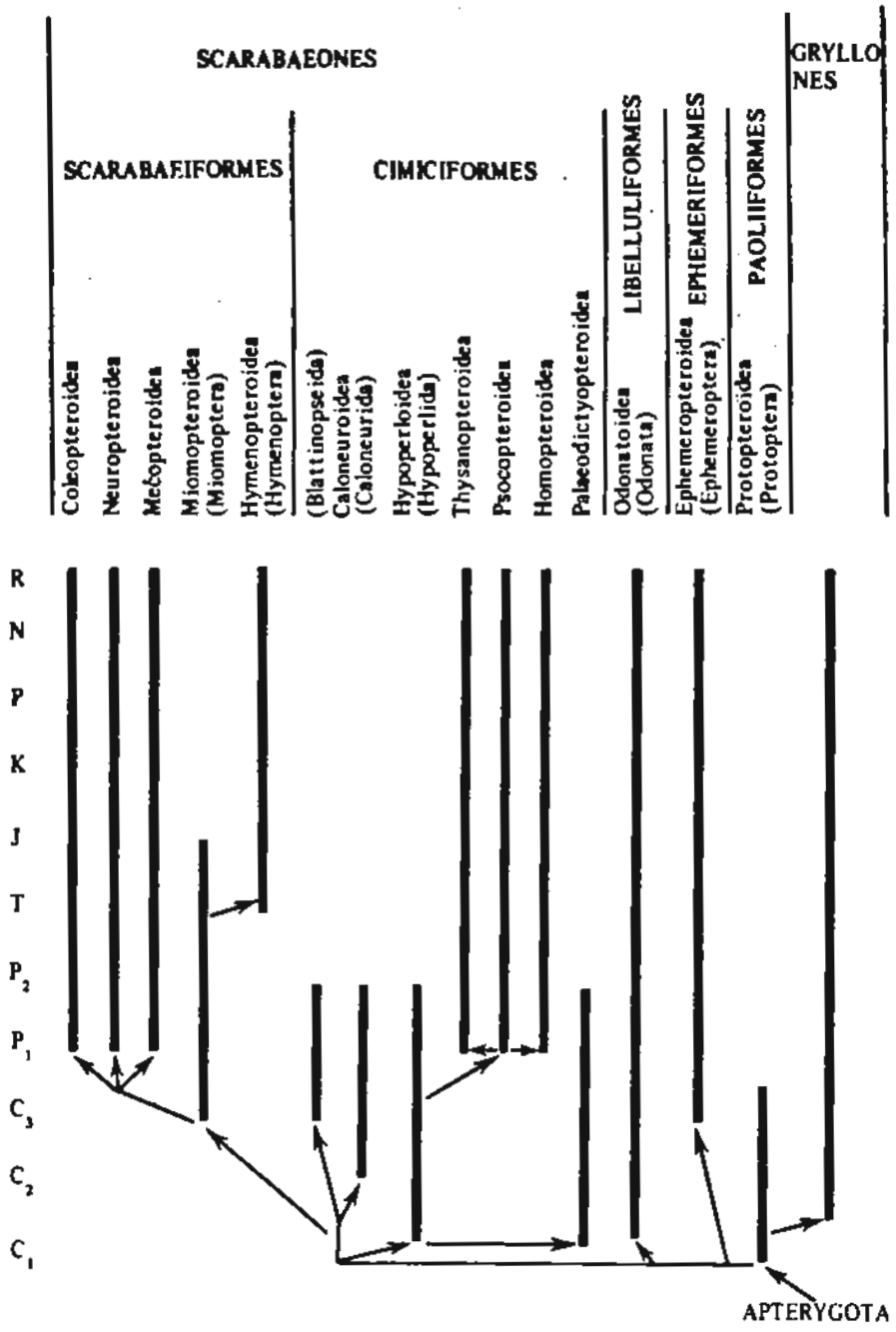
Chapter 2
The early evolution of Pterygota

In this and in the next chapter we shall attempt to substantiate the proposed system of winged insects (Pterygota) and their phylogenesis which differ markedly from those of A.V. Martynov (1925, 1937b, 1938) that are now universally accepted. The composition of many groups has been changed substantially. Furthermore, we use a number of names that have not been universally accepted as yet, even though they are not absolutely new. Some of these names were used by the author earlier (Rasnitsyn, 1976), and all of them were listed by B.B. Rohdendorf (1977). We find it nevertheless advisable to acquaint the readers with the main conclusions of that part of the work (table 1, fig. 5) in order to facilitate its understanding. A more detailed analysis of many of the problems raised here can be found in the work entitled Historical development of the class Insecta (1980). The systematic revision of the names of the older taxa of insects that has been proposed by B.B. Rohdendorf (1977) and is partly used here, is also outlined in that work.

As is well known, Martynov (1925, 1937b, 1938) divided Pterygota into a) Palaeoptera, whose wings remain within the plane in which they move in flight, so that in the state of rest they are permanently spread out or secondarily swung upwards; and b) Neoptera that are capable of moving their wings out of that plane and folding them on their abdomen. Neoptera are differentiated into Polyneoptera, Paraneoptera and Oligoneoptera. Many facts do not, however, fit into Martynov's system. In particular, there is a large number of characters common for Palaeoptera, Paraneoptera and Oligoneoptera, but contrasting them with Polyneoptera (Rasnitsyn, 1969, 1976). In the latter work the first three groups are set apart as the infraclass Scarabaeones, and Polyneoptera are classified as the infraclass Gryllones. In the process of folding their wings, Gryllones (=Polyneoptera) also fold under and turn over completely or almost completely the anal

region of their hind wing, sometimes with the exception of the first anal vein, rarely (in some Plecoptera) also excepting the base of the second vein. Their wings fold flatly or overlap, but never ... roof-like. Other features characteristic of Gryllones are the primitive structure of their mouthparts (in particular the lack of the piercing-sucking apparatus) and the normal development of their meso- and metathoracic sternal divisions proper (the absence of cryptosternum). The styles of the ninth segment in their males, if present, are not a functional part of their copulative apparatus, whereas the outer (third) valves in females are almost invariably a functional part of the ovipositor and participate with the two other pairs in the penetration of the substratum. Only ancient cockroaches (Vishnyakova, 1968) and many Protoblattodes (observations of Vishnyakova and of the author) still lack the true third valves. Moreover, their homologues, i.e. coxites and styles of the ninth segment, are short in these insects and do not form a protective case around the ovipositor. Their development is profoundly embryonized. In particular, the nymphs emerging from the eggs have compound eyes and almost always have fully differentiated legs. A less embryonized development persists to our knowledge only in some of the Early Permian forms, Lemmatophoridae and Atactophlebiidae in particular. In the former the nymphal tarsus is three- or four-segmented, while the tarsus of the imago comprises five segments (Carpenter, 1935). In Atactophlebiidae (Gurianovaella silphidoides Zal. from the Early Permian of the sub-Ural region) the tarsus of the early nymphs is three- if not two-segmented, while that of the late nymphs is composed of five segments. No nymphs with unsegmented tarsi are known in the insects whose imagos have segmented tarsi. p.17

Fig. 5.



The phylogenetic tree of Pterygota.

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TABLE 1

The classification system of winged insects (subclass Pterygota) adopted in this work

Rank of the taxon	Name	Equivalent in the system of Martynova-Rohdendorf (Rohdendorf, 1962)
Subclass	Pterygota	Same
Infraclass	Scarabaeones	Infraclass Palaeoptera+ the cohorts Paraneoptera and Oligoneoptera from the infraclass Neoptera
Cohort	Paoliiformes	None
Order	Ptoroptera	None (the families are in the order Paraplecoptera of the cohort Polyneoptera)
Cohort	Ephemeriformes	None
Order	Ephemeroptera	Same (within the infraclass Palaeoptera) According to Rohdendorf (1968)- the cohort Hydropalaeoptera in Palaeoptera
Cohort	Libelluliformes	None
Order	Odonata	Same (in the infraclass Palaeoptera)
Cohort	Cimiciformes	Cohort Paraneoptera+infraclass Palaeoptera (partly)
Superorder	Caloneuroidea	None
Order	Caloneurodea	Same (in the cohort Polyneoptera)
Order	Blattinopseida	None (the family is in the order Protoblattodea)
Superorder	Hypoperloidea	None
Order	Hypoperlida	None (families in different orders of different infraclasses and cohorts)
Superorder	Palaeodictyopteroidea	Same (in the infraclass Palaeoptera) (according to Rohdendorf, 1968 - the cohort Protorrhynchota in Palaeoptera)
Order	Palaeodictyoptera	Same
Order	Megosecoptera	Same
Order	Archodonata	Same

Order	Diaphanopterodea	Same
Superorder	Psocopteroidea	Same
Superorder	Thysanopteroidea	Same } cohort Paraneoptera
Superorder	Homopteroidea	Same
Cohort	Scarabaeiformes	Cohort Oligoneoptera
Superorder	Miomopteroidea	None
Order	Miomoptera	Same (in the cohort Polyneoptera)
Superorder	Coleopteroidea	Same
Superorder	Neuropteroidea	Same (including the order Glosselytrodea from the cohort Polyneoptera)
Superorder	Mecopteroidea	Same
Superorder	Hymenopteroidea	Same
Order	Hymenoptera	Same
Infraclass	Gryllones	The cohort Polyneoptera in the infraclass Neoptera

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Palaeoptera, Paraneoptera and Oligoneoptera (infraclass Scarabaeones) exhibit a different set of characteristics: the primary and most wide-spread position of folded wings is here roof-like with only a small portion of the anal region of the hind wing primarily folded under and turned over; that portion of the anal region commonly comprises one single vein (sometimes more, as in the case of the higher Trichoptera and Lepidoptera, but it is probably a secondary phenomenon);

the common base of the anal veins never turns over in the process of folding. The antagonism of the lateral and median longitudinal muscles of the mesathorax is here much more pronounced than in Gryllones. The mouthparts, particularly the maxillae and the labium, appear to be never as fully differentiated as those of most Polyneoptera (the most common phenomenon is the coalescence or reduction of the labial glossae); the sucking and piercing-sucking apparatuses are wide-spread. Primary characters of most Scarabaeones (excepting dragon-flies and May-flies) are the presence of the cryptosterna on the pterothorax, invagination of the sternal division and closure of the pleurites along the

p.18

median line. There is no previous record of cryptosterna in Palaeodictyopteroidea, but they are undoubtedly present, at least in Diaphanopterodea and Magasecoptera. In particular, the longitudinal sutures illustrated by Kukalova (Kukalova-Peck, 1972, Fig. 1) for Sylvohymen sibiricus Kuk. (Megasecoptera), are in fact the line of invagination of sternites, since the surface of the meso- and metathorax, which this researcher mistook for the dorsal surface, corresponds in reality to the ventral surface. This was established while studying the impressions, including that described by Kukalova. It was discovered at the same time that the "hollow processes of sternites" are at least partly (i.e. the median pairs of these processes) constituent elements of the furca (i.e. of the thoracic endoskeleton).

Furthermore, the styles of the ninth segment in the males of Scarabaeones form together with the coxites an important functional part of the copulative apparatus providing for fixation of the latter on the body of the female. The third valves of the ovipositor act primarily as a case of the ovipositor (in Palaeoptera, Paraneoptera, Miomoptera and Hymenoptera). The development of Scarabaeones is embryonized to a lesser degree than that of Gryllones. At the initial postembryonic stages the dorsal eyes are lacking (except in May-flies) and the tarsi either are not segmented at all or are segmented less fully than those of the imago (except for the cases where the number of segments in the imaginal tarsi is markedly reduced).

The characters distinguishing Gryllones (Polyneoptera) from all the other Pterygota (Scarabaeones, i.e. Palaeoptera, Paraneoptera and Oligoneoptera) appear to be considerably more convincing than those listed as evidence of the unity of the Neoptera and isolation of all or some of the Palaeoptera (Rasnitsyn, 1976). The boundary between the infraclasses has therefore been drawn between the former Polyneoptera and the other Pterygota forming the infraclasses Gryllones and Scarabaeones, respectively.

A.F. Emel'yanov (1977) recently advanced an alternative hypothesis. Proceeding from the disposition of folds (sutures) on the alar membrane, this author suggests that Plecoptera are

close to the roots of the insects with complete metamorphosis (Oligoneoptera). The other Polyneoptera occupy a similar position relative to Palaeoptera and Paraneoptera.

The weak point in this hypothesis is the instability of the characters used by A.F. Emel'yanov, that is particularly noticeable in Paleozoic insects. This applies to all the folds, but we shall examine only the fold associated with CuP, which is central to this author's hypotheses. According to Emel'yanov, in stoneflies (Plecoptera) and Oligoneoptera that fold is situated posteriorly of CuP, whereas in the other Pterygota it is located in front of CuP (we are really referring only to living insects, since Emel'yanov does not touch upon extinct forms in this respect). Indeed, the position of the fold characteristic of Plecoptera, is rarely observed in their ancestors, i.e. in Protoblattodea (sensu lato), where the fold is commonly located anteriorly of CuP. On the other hand in the second group of insects (Palaeoptera, Paraneoptera and most of Polyneoptera) the fold often passes behind CuP. For example, among the cicadas, in "Prosbolomorpha" the clavus (i.e. the part of the forewing located posteriorly of that fold) breaks off leaving CuP on the major portion of the wing. This is also characteristic of most Carboniferous cockroaches and of at least some of the most ancient Orthoptera belonging to Oedischiidae. Emel'yanov himself notes that in the recent cicadas the basal portion of CuP, sometimes nearly half of it, is also located anteriorly of the fold.

Adams (1958) also maintains that Plecoptera and their ancestors, i.e. Protoblattodea, are close to the insects with complete metamorphosis. However, the characters on which this author basis his hypothesis (the general appearance of the wing and the nature of its pubescence in Lemmatophoridae and Sialidae, and the tendency of some Plecoptera to form the third coxal joint characteristic of insects with complete metamorphosis) appear to be no more convincing than those separating Gryllones from Scarabaeones. p.19

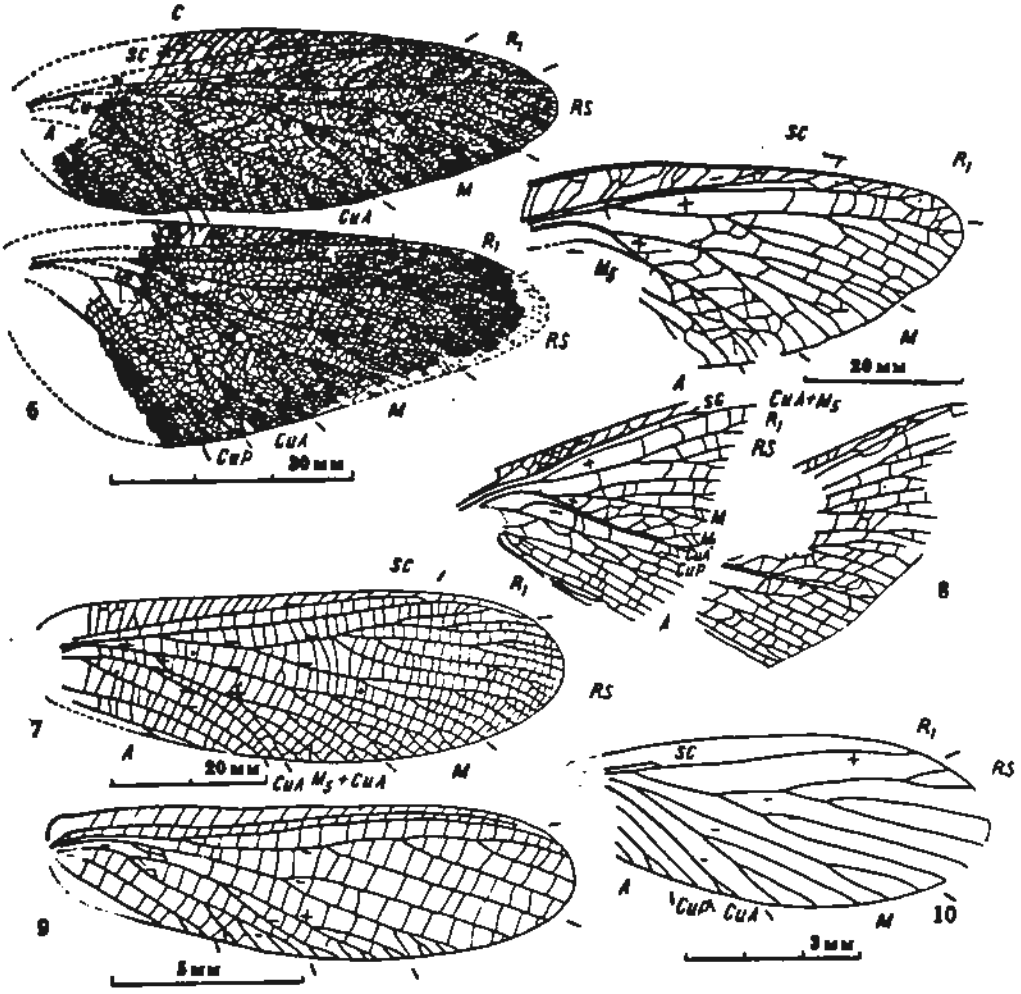

Fig. 6-9

Representatives of the order Protoptera

6-Zdenekia grandis Kuk.; Lower Carboniferous, Czechoslovakia;

7-Heterologus langfordorum Carp.; Middle Carboniferous, USA;

8-Evenkia archaica A.Rasn.; Upper Carboniferous, Tunguska basin;

9-Hapaloptera gracilis Handl.; Middle Carboniferous, USA

(6-from Kukalova, 1958; 7 and 9-from Carpenter, 1965; 8-from Rasnitsyn, 1977a).

Fig. 10 Metropator pusillus Handl.; Lower Carboniferous, USA (from Carpenter, 1965).

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The paleontological history of winged insects begins in the Namurian, the last age of the Early Carboniferous epoch.* Namurian insects are not numerous and are known only from odd wings. They are, however, extremely interesting in that those of their characters that are accessible for the analysis, permit us to regard most of these insects as a group ancestral to all the Pterygota.

We are referring to the order Protoptera established by A.G. Sharov (1966a) for the family Paoliidae (fig. 6), which was previously included into Protorthoptera and was regarded still earlier as part of Palaeodictyoptera (Kukalova, 1958a; Carpenter, 1965; Carpenter, Richardson, 1971).

Many other Carboniferous insects, mainly those amalgamated in the past within the superfamily Cacurgoidea (see Rohdendorf, 1962) or treated as forms close to Cacurgidae, exhibit p.20
a marked resemblance to Paoliidae. Some of them [Cacurgidae (fig. 7), Evenkiidae (fig. 8), Herdinidae (table II, fig. 5), Stygneidae, Omaliidae and Hapalopteridae (fig. 9)] were already mentioned earlier as possible members of the order Protoptera (Rasnitsyn, 1976, 1977a). This list can be expanded considerably, but it must be kept in mind that the anterior wings alone are not a sufficient criterion for classifying a form with Protoptera; nor are the hind wings by themselves, though they are indispensible if we are to do so. The decisive argument should be the body structure, particularly the structure of the sternal surface of the thorax and that of the genitals of both sexes (see farther on). But a large majority of the presumed representatives of Protoptera are known only from their forewings, on the basis of which we can detect smooth transitions to various lower Scarabaeones, particularly to the orders Hypoperlida and Blattinopseida described farther on,

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* Since there are many Namurian insects for which the exact stratigraphic position within the Namurian is not indicated, that stage is tentatively treated here within its broad limits, including the Namurian C.

as well as to Gryllones. Aenigmatodes Handlirsch and the group Mixotermitodea are particularly close to Hypoperlida and may easily prove to be members of that order. Hapaloptera Handlirsch and Limburgina Laurentiaux also display a considerable similarily to Hypoperlida. Metropator Handlirsch that is discussed in detail farther on, resembles somewhat even Oligoneoptera. Cacurgidae and the groups close to them of the type of Coselia Bolton, Omalia van Beneden et Coemas, Prototettix Giebel, Protocollaria Brongoniart, Nacekomia Richardson, Homalophlebiidae etc., are similar to Paoliidae, as well as to the lower Protoblattodea of the type of Narkemidae, to Sthenaropodidae (Protorthoptera), and even to the primitive cockroaches of the genus Aphthoroblattina. Of course, this merely confirms the ancestral nature of Protoptera, but it also obscures the boundaries of that order. In particular, the only forms among those listed above that can be referred with confidence to Gryllones, are Aphthoroblattina, Narkemidae and Sthenaropodidae for which the hind wings with the anal flabellum that curls under are known. On the other hand Paoliidae, Evenkia, Herdina, Metropator, Limburgina and certain other forms that are believed to be close to "Mixotermitodea" (Kliveria Handl.), can be excluded with equal confidence from among the Gryllones on the basis of their hind wings that are devoid of the flabellum. This character is not, however, a sufficient criterion for determining the systematic position of these forms more accurately.

Because of the circumstances outlined above, it is impossible to characterize Protoptera in a clear-cut manner. We can merely note that, judging from the attributes characteristic mainly of Paoliidae, Evenkiidae and Cacurgidae, the order discussed has the following, largely primitive, characters.

Protoptera are characterized, as a rule by large (5-10cm in length) and broad wings that are weakly specialized from the mechanical viewpoint, are not costalized, may be somewhat pointed at the top and have a convex (domed) anterior margin. The anterior wings are more or less lanceolate and subsymmetrical, while the posterior wings are rather narrowly triangular in shape. Venation is weakly differentiated with regard to both the thickness of the

veins and their position in the membrane. Even the radial vein which is distinctly thickened in other insects (at least in the pair of the wings playing the major role in flight), is here often of the same thickness as the other veins. As a rule R and CuA alone have a perceptibly raised (prominent) position in the membrane; SC is distinctly depressed, as is, though to a lesser degree, CuA; and the other veins are more or less neutral or may have a gently depressed (concave) position. Judging from the photographs in Kukalova's work (1958a, plate 1, fig. 2; plate 2, fig. 1), in the hind wings of Paoliidae all the veins posteriorly of R (including CuA, CuP and A) are gently and almost identically depressed. With regard to the branching of their veins, structure of the veins and their position relative to the membrane, and with respect to the instability of the venation (which may vary markedly from the left to the right wing in the same pair of wings of an individual), the wings of many Protoptera resemble the leaves of plants more closely than the wings of any other insects. This resemblance may be intensified by the irregular meshwork of the archedyction.

Protoptera folded their wings in repose, a circumstance evident from the position of the wings in the impressions of Sustaia impar Kuk. (Kukalova, 1958a) and Cacurgus spilopterus Handl. (Handlirsch, 1906). The exact manner in which the wings were folded is not known, but their position was probably roof-like. In any event the gently expanded anal region of the hind wing did not fold under in Paoliidae and Evenkiidae, which testi- p.21
fies that the folding mechanism in these insects was different from that of Gryllones.

Some of the characters of venation in Evenkiidae are especially significant, since they have also been observed in many other groups of insects. We are referring in particular to the differences in the position of the base of RS in the anterior and posterior wings and especially to the structure of CuA in the hind wing. In the posterior wing of Evenkia archaica A. Rasn. RS branches off R much more proximally than in the anterior wing. The same character has been observed in some of the Paoliidae

(Kukalova, 1958a, Abb. 1-2) A more marked heteronomy of the wings with respect to the position of the base of RS is characteristic of both Gryllones (many cockroaches, Protoblattodea, Plecoptera and some Orthoptera) and Scarabaeones (Hypoperlida and Blattinopseida among the orders described below, and many Oligoneoptera: Mecoptera, Trichoptera, Rhaphidoidea, some Neuroptera, particularly representatives of Berothidae, and, to a lesser extent, Megaloptera).

CuA is commonly prominent in the wings of insects and is somewhat raised relative to the nearby veins. This is also the case with the fore wings of Protoptera. In the hind wings of Paoliidae CuA may, as was mentioned earlier, have at least a gently concave position similar to that of the other veins. In Evenkiidae it is more sharply depressed which may be due to the presence of a distinctly raised, though very weak posterior branch of the median vein designated as M_5*, right in front of it. In the wings of insects M_5 commonly merges with CuA leaving free only its base in the form of a short obliquely or even transversely oriented prominent vein, which may disappear later on. It would appear that it is precisely M_5 that is responsible for the prominent position of CuA (or, more precisely, M_5+CuA), and its effect has

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* This vein owes its name to the notion that in a typical case the median divides into two main trunks (MA and MP), each of which divides dichotomously once again producing four branches (M_{1-4}). Given this approach, the vein discussed is the fifth branch of the median (Tillyard, 1924b). Of course, it deserves much more to be designated as MP (media posterior) and to be contrasted with the rest of the system (MA - media anterior, respectively) because of its having branched off such a long time ago and of its being located anteriorly of all the other branches of M. In some cases it it, indeed, referred to as MP (particularly in cockroaches), but commonly this designation is reserved for the branch of the median extending anteriorly of it. The latter may be (Palaeodictyopteriodea, Ephemeroptera) distinctly differentiated and has then a concave position in contrast to the prominent MA. The use of MP is thus ambiguous and this designation commonly refers to a different vein from the one discussed. As far as we know, the symbol M_5 is used only with reference to the vein discussed, which compels us to accept this designation.

been noted in many groups of Pterygota. The depressed CuA of the posterior wing that is commonly accompanied by a prominent sclerotized fold along its anterior edge or is located on a convex fold of the membrane, is often described as CuA+CuP or simply CuP in Trichoptera (Platychoristidae; Carpenter, 11930; see Sukachev, 1976, regarding the classification of this family with Trichoptera), Metropatoridae (Carpenter, 1965; see more detail regarding this family farther on), Miomoptera (Carpenter, 1933, 1965) and Mecoptera (Ponomarenko, Rasnitsyn, 1974) and is characteristic of many other forms of Mecoptera and Trichoptera, as well as of Blattinopseida, Hypoperlida, Homoptera Archescytinidae and Psocoptera Psocidiidae, and, among Gryllones, of most, if not all, the representatives of Protoblattodea.

The structure of M_5 and CuA in Evenkia suggests the possibility of an even more primitive condition persisting in the other Protoptera: a powerful, prominent branching M_5 and a depressed CuA that is connected with the former only by an obliquely oriented vein (probably its anterior branch) and is not ramified any further. This interpretation suggests itself, for example, for the venation of the Middle Carboniferous Heterologus langfordorum Carpenter (see fig. 7).

As was mentioned earlier, the body structure of Protoptera is not known, but if they really were ancestors of the other Pterygota, the structure of their body can be partly reconstructed. The mouth must have had the full complement of its parts: two pairs of palpi, a maxilla with well-developed galea and lacinia, and a labium with well-defined glossae and paraglossae. The thorax with fully developed sternal divisions and completely differentiated legs. The abdomen with the customary number of segments, with segmented cerci and, possibly, with a paracercus. p.22
The structure of the ovipositor is similar to that of Thysanura, particularly in that the coxites of the ninth segment do not form the third valves as yet, even though they may be close to the first two pairs of valves; the ovipositor was probably of the cutting (sectorial) kind adapted to shallow oviposition in plant tissues, as is the case in many representatives of Jugatae, Odonata and lower

Hymenoptera. The styles of the ninth segment were present in the males, but occupied a position similar to that recorded in Thysanura and were not used for fixation on the body of the female.

Ontogenesis corresponded to archaemetaboly: a larva hatched from the egg had an undifferentiated tarsus that may not even have been separated from the tibia, with a simple praetarsus, a reduced segmentation of the antennae, and without the external rudiments of genitals or wings. As the larva developed, its tarsi and antennae became gradually differentiated and there appeared rudimentary genitals and wings. The wing cases were initially subtriangular and fixed; subsequently they gradually increased in size acquiring a shape that resembled more closely the imaginal wing, and the ability to fold. Molting persisted even after the appearance of flapping flight. The wings of Evenkia archaica A. Rasn. may have belonged to flying subimagos of this kind (Rasnitsyn, 1977a). The early postembryonic stages of Protoptera may have lived in crevices in the substratum and fed on pollen (dispersed or extracted from shed sporangia), even though it cannot be ruled out that they developed completely in trees, where they extracted pollen or ovules directly from sporangia.

As regards the taxonomic position of Protoptera, they undoubtedly merit to be classified as a separate cohort Paoliiformes in spite of the indeterminate boundaries of their order. That order can also be classified as a separate infraclass, but, keeping in mind that from the morphological and ecological viewpoint the transition from Protoptera to Scarabaeones should be smoother than their transition to Gryllones, and that the characters distinguishing them from the latter group (the structure of the hind wing) can be fixed in fossil material with a considerably greater confidence than their differences from the former group, it appears advisable to include Paoliiformes into Scarabeones.

Among the many Carboniferous insects that are believed to be close to Protoptera we should focus especially on Metropatoridae.

This family is known from one single impression from the Lower Namurian in the USA (see fig. 10) and is among the oldest insects. It is similar to Paoliidae because of the somewhat incurved position of all the veins observable posteriorly of its R (we are referring to the hind wings) and resembles Evenkiidae in the branching pattern of its RS and M. However, its small stature, unusually small (7mm) for such ancient insects, its markedly reduced anal region, its very short and simple SC, and its CuA that has one single short distal bifurcation and appears to be more markedly depressed than either RS or M, sharply distinguish Metropator Handl. from typical Protoptera and bring it closer to the other Scarabeones (Hypoperlidae, Miomoptera and Mecopteroidea). Its resemblance to the two latter groups has already been mentioned in the literature. Metropatoridae were included for a long time into the order Mecoptera until Carpenter (1965) transferred them to Miomoptera on the grounds that such an early (in the Early Namurian!) appearance of insects with complete metamorphosis should be supported by much more reliable evidence than it is possible in the given case. It turned out, however, that Miomoptera belong to Oligoneoptera (see below). The irregular branching of RS and its later (than in the hind wings of Miomoptera) divergence from R, the early and repeatedly branching M, and the markedly reduced anal region of Metropatoridae also testify against their being related to Miomoptera. It appears more probable that Metropatoridae are among the numerous descendants of typical Protoptera that evolved in the same direction as Hypoperlidae, Blattinopseidae and Miomoptera. Metropatoridae may be close to the ancestors of one of these groups or to their common ancestor.

From now on we shall focus mainly on the evolution of Scarabeones, since Hymenoptera, which are the main subject of our study, belong to them. But prior to proceeding with that problem and before we abandon the extensive group of Gryllones, we shall endeavour to visualize the main processes which led to their appearance.

Gryllones may have evolved as a result of their gradually weakening association with generative organs of Gymnospermae and because of their transition to saprophagy and predation on the one hand and to a more sheltered mode of existence (in the ground cover, under the bark or in decayed wood, particularly in accumulations of large remnants of dead plants, such as wind-fallen trees) on the other. The change to a sheltered existence may have been prompted by the appearance of air-borne predators, such as dragon and demoiselle flies, which may have appeared somewhat earlier than Gryllones (the earliest remains of Odonata are known from the Upper Namurian, remains to Gryllones - since the beginning of the Middle Carboniferous; Rohdendorf, 1969*).

The existence in cramped, narrowly confined situations led to an intensive selection for a more compact way of folding the wings than the roof-like pattern. It was scarcely possible to achieve the desired effect by way of a simple decrease in the size of the wing, since the primitive Gryllones appear to have had large measurements and a relatively imperfect flying apparatus that called for a large wing area, and because of the low frequency of beating (flapping) the wings. Given the circumstances, a more effective adaptive solution would have been to change to the streamlined appressed mode of folding the wings that often altered eventually to the flat folding**, with nearly all of the anal region of the hind wing curled under.

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* Durden's report (1964) of the earlier appearance of Gryllones (cockroaches) at the very end of the Late Namurian demands that the deposits in question be dated on the basis of more reliable criteria.

** These two modes of wing folding are not clearly separated and have historically been readily interchangeable. They are therefore treated together in the further account.

The latter circumstances has predetermined in many ways the further evolution of the infraclass, since this mode of folding, supplemented by the fan-like folding of the anal region that was curled under, made it possible to increase considerably the area of the hind wing whenever necessary and to intensify thereby the flight without the need to improve the mechanism setting the wings in motion. Of course, this course of development of flight can scarcely be regarded as highly promising, but, given the sheltered mode of existence of the insects which weakened the selection for intensified flight, it may have been adequate. The means employed during the subsequent transition to the open mode of life were of the circuitous nature: the jump as an additional means of escape from the enemy (as in Orthoptera), the cryptic colouring; the body shape and behaviour that were often accompanied by the weakening or loss of flight (as in Phasmides and Mantidae), or the ephemeral nature of the imago (as in Plecoptera).

The relatively minor role of flight in the life of Gryllones also predetermined the resemblance of their preimaginal stages to their imagos. This led to their morphological convergence which found its expression in the embryonization of ontogenesis that is so characteristic of gryllones, and in the adultization* of their postembryonic stages of development (Rasnitsyn, 1965a, 1969). See the historical development of the class Insecta (1980) for a more detailed account of the evolution of Gryllones.

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* By "adultization" we refer to the increasing resemblance of the given ontogenetic stage to the later stages, and by "juvenilization" to their increasing resemblance to the earlier stages of development (Tikhomirova, 1976). These terms are used because of the vagueness or even ambiquity of the terms "embrionization", "de-embryonization", "imaginization", etc. referring to the ontogenetic stages. When applied to the process of development as such, the meaning of these terms is equivocal (see also Rasnitsyn 1965a).

The evolution of Scarabaeones, unlike that of Gryllones, involved primarily the improvement of flight and was accompanied by the restructuring of the mechanisms moving the wings. This may account for characters such as the presence of cryptosterna or the sharply defined antagonism of mesothoracic muscles. Furthermore, the differences in the main modes of locomotion of the imagos and preimaginal stages stimulated their ecological and, consequently, morphological divergence. The processes of the embryonization of development were inhibited accordingly.

Chapter 3 p.24

Evolution of the infraclass Scarabaeones

Odonata and Ephemeroptera stand apart from the other members of the infraclass. They have preserved the primitive structure of the thorax (the absence of the cryptosternum), but are specialized in other respects. The two orders are similar in a number of characters, the nature of which makes it impossible, however, to infer that they are closely related. Indeed, the primitive structure of the thorax that is characteristic of both these orders, is no more evidence of their common origin than any other symplesiomorphy*. Adaptations of Odonata and Ephemeroptera larvae to the aquatic mode of life are different and testify rather to their having changed to developing in water independently. The loss of the ability to fold wings also occurred on account of different processes in the two orders: in Ephemeroptera it is related to the ephemeral nature of the imago, the function of which is restricted essentially to the nuptial flight and oviposition, and in Odonata to the development of the adult insect into an active aerial predator. It is highly likely that Odonata and Ephemeroptera are independent evolutionary branches.

The view that Odonata and Ephemeroptera belong to the common stem of Scarabaeones, i.e. that they diverged from Protoptera as part of the stem including the other members of that infraclass (with the exception of Protoptera), is supported by that the styles of the ninth segment have been modified in the males of Epheroptera to a portion of the copulative apparatus and in females of Odonata to the case of the ovipositor. In Ephemeroptera the ovipositor has been reduced, and the function of the styles in females of their ancestors remains unknown, but the fact that their reduction coincides with the reduction of the ovipositor is in itself indirect evidence of the styles having been incorporated into the ovipositor and shows that Ephemeroptera resemble in that characteristic Odonata on the one hand and higher Scarabaeones on the other. Nor can the reduction of the primitive copulative apparatus in Odonata be used as a criterion for inferring its

*=symplesiomorphism. Translator.

original structure. However, the compact disposition of its rudiments (Makhotin, 1934) that is characteristic of most Scarabaeones (with the exception of Ephemeroptera) and correlates in these insects with the development of a separate, more or less mobile genital capsule, evidences that Odonata resemble higher Scarabaeones even more closely than Ephemeroptera. This suggests that Odonata branched off the common stem of the infraclass even later than Ephemeroptera. Another evidence in support of that inference is the late appearance of ocelli in the ontogenesis of Odonata. This is also the case in Paraneoptera and Oligoneoptera, where, in contrast to Thysanura, Ephemeroptera and Gryllones the ocelli appear at the very first postembryonic stage (see fig. 3).

Both Odonata and Ephemeroptera merit the rank of separate cohorts (Libelluliformes and Ephemeriformes, respectively). As was mentioned earlier, the former are known since the Late Namurian and are the oldest order of insects persisting to our days. Even though Ephemeroptera are presumed to have diverged earlier, they have been recorded with confidence only since the Late Carboniferous. This does not necessarily mean that their geological record is incomplete. It is entirely possible, for example, that the ancestors of Ephemeroptera acquired the attributes characteristic of that order only by that time.

Insects with complete metamorphosis form a compact group within the Scarabaeones (the cohort Scarabaeiformes= Oligoneoptera). They are distinguished most of all by a sharp differentiation of the ontogenesis at the stages of predominant morphogenesis (egg and pupa), feeding and growth (larva) and reproduction and dispersal (imago) (Rasnitsyn, 1965a). Moreover, the degree of embryonalization of the ontogenesis (adultization of the initial postembryonic stages) is minimal and is comparable only to that of Ephemeroptera among the recent Pterygota. Of the morphological characters common for the imagos of all the Scarabaeones, we could mention perhaps only the appearance of the third medial joint between the meso- and metacoxae and the thorax. The composition and structure of the cohort are discussed farther on.

Among the other Scarabaeones there have been identified two large groupings: Paraneoptera and Protorrhynchota. The former group comprising Psocopteroidea, Thysanopteroidea and Homopteroidea*, was set apart by Martynov (1925) as one of three subdivisions of Neoptera. The cohort Protorrhynchota was established by B.B. Rohdendorf (1968) for the Paleozoic orders of Palaeoptera grouped around Palaeodictyoptera. In addition to that order, it also includes Megasecoptera, Archodonata and Diaphanopterodea, and is contrasted by Rohdendorf with the cohort Hydropalaeoptera (Ephemeroptera+Odonata). The criterion on the basis of which Protorrhynchota have been set apart, is the structure of their mouthparts modified to a piercing-sucking proboscis. p.25

Rohdendorf believed the proboscis of Protorrhynchota and Homopteroidea to be identical in structure and assumed that Protorrhynchota were direct ancestors of Homopteroidea and of all the Paraneoptera. The arguments advanced (Sharov, 1973) against Rohdendorf's hypothesis are based on the differences in the structure of the proboscis: a) in Homopteroidea the stylets are protected by a case formed by the labium, and in Thysanopteroidea - by a case formed by the labrum, while in Protorrhynchota they are protected only by the maxillary and (at least in Diaphanopterodea) labial palps; and b) the absence of proboscis in Psocoptera. It is, indeed, virtually impossible to derive all the Paraneoptera from Protorrhynchota. The opposite hypothesis postulating that

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* Zoraptera also belong to Paraneoptera, but even the most important common characters of these insects and Paraneoptera [the reduced number of malpighian tubes, free ganglia of the nerve cord and segments of the tarsi (see Kristensen, 1975)] appear to be as unreliable than those which they have in common with Gryllones (first of all the structure of the lower thoracic surface and, in particular, the absence of cryptosterna). On the other hand not all the characters distinguishing (in Krestensen's opinion, l.c.) Zoraptera from Paraneoptera are of that kind (the ocelli are developed not only in the nymphs of Zoraptera, but also in those of Paraneoptera: e.g. in late nymphs of Cicadidae). The problem regarding the position of Zoraptera in the system of insects needs to be studied farther.

Protorrhynchota originated from Rrhynchota, is equally unacceptable, since even the most primitive representatives of the latter (Archescytinidae) have a specialized proboscis and appeared much later than Protorrhynchota (in the Permian). It is nevertheless quite probable that Protorrhynchota and Paraneoptera are related phylogenetically, as is suggested by a number of structural characters of the order Hypoperlida.

The order Hypoperlida comprises a varied and probably fairly large group of Paleozoic insects with characteristics of advanced Scarabaeones (the thorax with cryptosterna, the primitive roof-like folding of the wings, the hind wings without the anal lobe folding under, the ovipositor with a protective case). These insects have certain features in common with Paraneoptera and Protorrhynchota (their head and mouthparts tend to be elongated in a manner identical to that observed among the Permian Psocoptera; it may be assumed that this elongation is an intermediate stage in the development of the proboscis in Protorrhynchota).

Hypoperlidae, the central family of the order (Rasnitsyn, 1977a), has been recorded with confidence since the Late Carboniferous (fig. 11), but it attains a particularly great diversity in the Permian (figs 12-16). Moreover, the forms described are but a fraction of the material representing that group in the collection.

Hypoperlida were described as part of Paraplecoptera (Martynov, 1928), but Sharov (1961) noted that they differed sharply from both Paraplecoptera* and Plecoptera, and pointed out that their systematic position should be revised.

Many members of that family (Dinopsocus Martynov=Martynopsocus Karny, Kaltanelmoa Rohdendorf, Fatianoptera O. Martynova) were described as separate families within different orders of insects (Psocoptera, Diaphanopterodea and Raphidioptera, respectively) but

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* Subsequently Protoblattodea (Sharov, 1968).

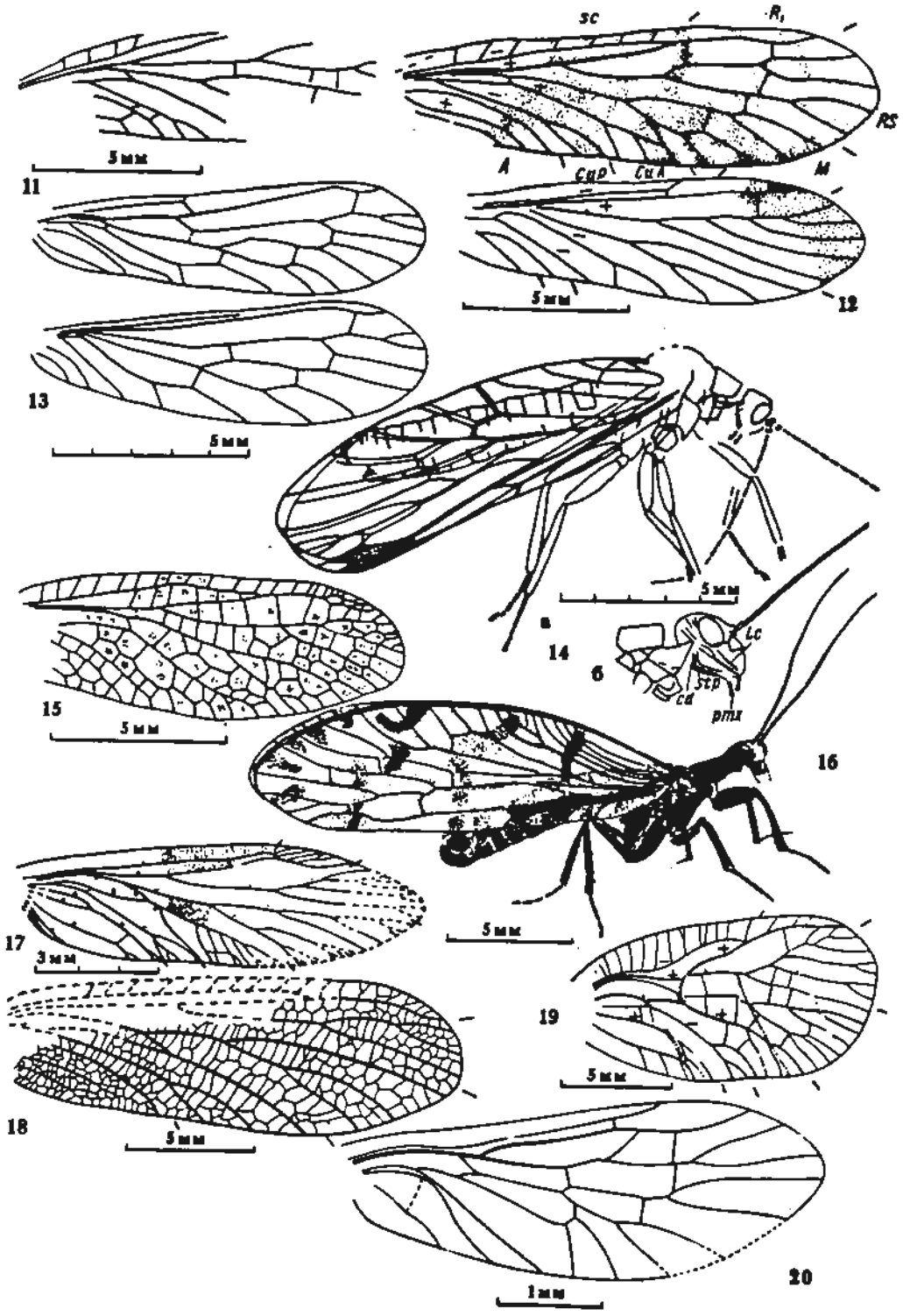
at least for Martynopsocus it was already noted that it resembled Hypoperlidae (Sharov, 1961).

Reliable finds of Hypoperlida are not known outside the USSR, but some of the Carboniferous insects, including Namurian forms from Europe and North America, [Ampeliptera Pruvost (fig. 17) and Aenigmatodes Handlirsch (fig. 18) in particular] may belong to that order.

Other Carboniferous insects, some of which were mentioned earlier with reference to the order Protoptera, may also turn out to be close to Hypoperlida. We are referring to Limburgina Laurentiaux, Protoprosbole Laurentiaux (fig. 19), Metropator Handlirsch (see fig. 10), "Mixotermitodea", Pseudohomotethus Handlirsch, Climaconeura Pruvost, Emphyloptera Pruvost and Hapaloptera Handlirsch (see fig. 9). p.27

The general habit characteristic of Hypoperlida is similar to that of Neuroptera and Mecoptera: body light and slender, folding of membranous wings roof-like, wings homonomous in form, but with a characteristic heteronomy of venation that has been partly inherited from Protoptera of the type of Evenkia and is practically identical to that of many insects with complete metamorphosis (particularly Miomoptera). In the anterior wings RS diverges off R considerably more distally than in the posterior wings, CuA is sharply outcurved (prominent) and CuP is just as sharply depressed, whereas in the hind wings CuA is distinctly incurved (depressed), even though it is often located on the convex fold of the membrane, while CuP is almost neutral (perhaps as a result of its confluence with the anterior branch of A). RS is normally strictly crestate backwards, commonly with 3-4 branches. M is free (does not unite with CuA at the base), usually with 2-4 branches; as a rule, it starts branching late; in the event of its having three ends, M is pectinate forward, but when it has four ends, it divides dichotomously. M_5 is in the form of a characteristic short and oblique, less often transverse vein between M and CuA. CuA with a short bifurcation (sometimes with three ends). CuP is simple or branches out before reaching the summit. Anal veins few in number.

Figs.11-20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Lc
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cd
pmx
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1мм

Representatives of the family Hypoperlidae
11-Tshunicola carbonarius A. Rasn.; Upper Carboniferous, Tunguska basin; 12-Hypoperla elegans Mart.; Upper Permian, Arkhangel'sk region; 13-Martynopsocus arcuatus (Mart.); Upper Permian, Arkhangel'sk region; 14-Hypoperlopsis splendens G.Zal.; Lower Permian of the sub-Ural region; a-general view, b-head; 15-Fatianopter mnemonica O.Mart.; Lower Permian of the Tunguska basin; 16-Tshekarodobia osmylina A.Rasn.; Lower Permian of the sub-Ural region; reconstruction. (11-From Rasnitsyn, 1977a; 16-Original drawing by A.G. Ponomarenko; 12-15-Originals; 12-Soyana; a-specimen 117/968, b-specimen 117/2285; 13-Soyana; a-117/2187, b-3353/459; 14-Chekarda; a-specimen 1700/3298, b-1700/1880; 15-holotype).

Figs. 17-19
Insects believed to be close to Hypoperlidae
17-Ampeliptera limburgica Pruvost; Lower Carboniferous, Holland; 18-Aenigmatodes danielsi Handl.; Middle Carboniferous, USA; 19-Protoprosbole straeleni Laur.; Lower Carboniferous, Belgium; (17-From Kukalova, 1958; 18-Original drawing by A.G. Sharov from the photograph of the holotype; 19-From Rohdendorf et al., 1962).

Fig. 20
Permopsocus latipennis Till., a representative of the suborder Permopsocida; Lower Permian, USA (from Tillyard, 1926).

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Antennae and legs slender, long. Head small, with gnawing mandibles and, possibly, with elongated baculiform laciniae of the maxillae (see fig. 14b). Pterothorax homonomous. Ovipositor of the sectorial type; its third valves form a protective case (see fig. 16). The structure of male genitals unknown. Cerci short, single-jointed. From the viewpoint of their bionomics Hypoperlida are believed to have been plant dwellers which retained their trophic links with generative organs of plants.

Hypoperlidae are very similar in their characteristics to primitive Paraneoptera, in particular to Psocoptera. The similarity of venation in some of their representatives with that of Permian Psocidiidae is particularly striking (fig. 20). It is possible that Hypoperlida were direct ancestors of Psocoptera, hence of all the Paraneoptera, particularly if we take into account that Hypoperlida are an older order. No Paraneoptera have been recorded with confidence in the Carboniferous. The validity of the classification of Protoprosbole Laur. and two other Carboniferous insects (Archeglyphis Mart. and Blattoprosbole B.-M.) with Jugatae is questionable; the latter of the two is probably a cockroach (Sharov, 1966a). Archeglyphis is known from one single poorly preserved impression displaying no clear-cut resemblance to Jugatae, and Protoprosbole, judging from its venation, is very close to Hypoperlidae. If, however, the assumption regarding the presence of elongated baculiform laciniae in Hypoperlidae proves to be correct, the close relationship of that group to Paraneoptera will be practically beyond doubt.

In spite of the probable kinship of Hypoperlidae and Psocoptera, it would be rather unwise to refer them to that order or even to the group "Paraneoptera". The most characteristic feature in the evolution of Paraneoptera is their transition to an increasingly more perfect parasitism of plants with feeding primarily on generative organs (Psocoptera of the suborder Permopsocida with their elongated rostriform head, Vishnyakova, 1976; thripts (Thysanoptera) feeding on pollen even now, see Grinfeld'd, 1962; primitive Jugatae of the family Archescytinidae with a distinctive structure of the ovipositor that led Bekker - Migdisova, 1972, to infer that they laid eggs inside young cones of gymnospermous plants, from which their larvae emerged once the cones opened). Only later did Paraneoptera change to feeding on vegetative organs of plants (in some cases even to predation at a later date) or to mycophagy (recent Psocoptera). Depending on their trophic specialization, the importance of flight decreases to a greater or lesser degree and the insects may develop the ability to hop as a compensation. As a result of this their general

habit alters: the body becomes more compact and stout already in Psocoptera and that body shape persists in most Paraneoptera. We feel that the transition to a less mobile mode of life is the most logical point for drawing the boundary of Paraneoptera. The presence of cerci in Hypoperlidae and their lack in Paraneoptera may serve then as the formal diagnostic character.

If, however, we accept the presence of baculiform laciniae in Hypoperlidae as an established fact and draw the boundary of Paraneoptera at the point, where that character appears, we will probably have to include into that group of Paraneoptera the Protorrhynchota, may have inherited elongated laciniae from their common ancestor with Hypoperlidae. This amalgamation undoubtedly makes sense. Moreover, the boundary between the resultant large group (which also includes certain other orders that are discussed farther on) and the other Scarabaeones is more sharply defined than any of the boundaries that can be drawn within it, and corresponds better to the boundaries between the different cohorts. This group (Paraneoptera+Protorrhynchota+Hypoperlida etc.) can be classified as one single cohort Cimiciformes, but it would differ then very markedly from Paraneoptera in Martynov's interpretation.

The large hiatus between Hypoperlidae and Protorrhynchota is filled to a certain degree by the families Synomaloptilidae and, Strephocladidae with close groups (Tococladidae, Nugonioneuridae and Permarrhaphidae), perhaps also by Homeodictyidae. Synomaloptila Martynov (fig. 21), a representative of the former family, resembles fairly closely Hypoperlidae with regard to its venation, but, similarly to the other members of the family, has a different general habit (figs 22-24). Stature large; body long, but rather heavy; wings long and folding flat on the abdomen. Legs powerful, of the gripping kind found in many of the beetles living on plants (femur dentate, segments of tarsus broadly bilobate, ungues large; in contrast to beetles, a very large arolium is present). Head markedly elongated and pointer anteriorly in the form of a beak; moreover, the slender and long sublancetoid mandibulae serrated along the inner edge, form the summit of the "beak". The

"beak" also includes the maxillae (by analogy with Psocoptera, probably their laciniae). These structures, unlike those of Hypoperlidae, are here distinctly and markedly hypertrophied, considerably more markedly than those of Hypoperlidae, and are sublancetoid in shape. ... They are serrated along the inner edge, are forked at the base, and occupy more than half the length of the head. Judging from the structure of their head and legs, Synomaloptilidae may have lived on vegetation and fed on the contents of ovules of gymnospermous plants (Rasnitsyn, 1977a). Sharov (1973) infers a similar mode of feeding for Protorrhynchota, except for the fact that they had a true piercing-sucking proboscis and were probably obliged to suck out rather than gnaw out the contents of the ovules, hence to feed on younger immature ovules.

With regard to their mode of life and head structure, Synomaloptilidae could have been ancestors of Protorrhynchota, but for the following obstacles: a) the flat folding of the wings, from which we cannot derive the roof-like folding pattern characteristic of Diaphanopterodea; and b) the later (in the Permian) appearance of the family in the geological record. The former obstacle is removed by the existence of the family Permarrhaphidae (=Strephoneuridae syn.nov.*) that is similar to Synomaloptilidae in the structure of its head and legs (femora dentate, tarsi with powerful ungues and arolium), but retains the roof-like folding of the wings. Its venation differs markedly from that of Synomaloptila Martynov, and resembles more closely that of the other Synomaloptilidae. It is significant that the posterior branch of M is distinctly depressed in Permarrhaphidae. The same characteristic, though less clearly defined, has been observed in Mycteroptila. It may be p.30

p.29

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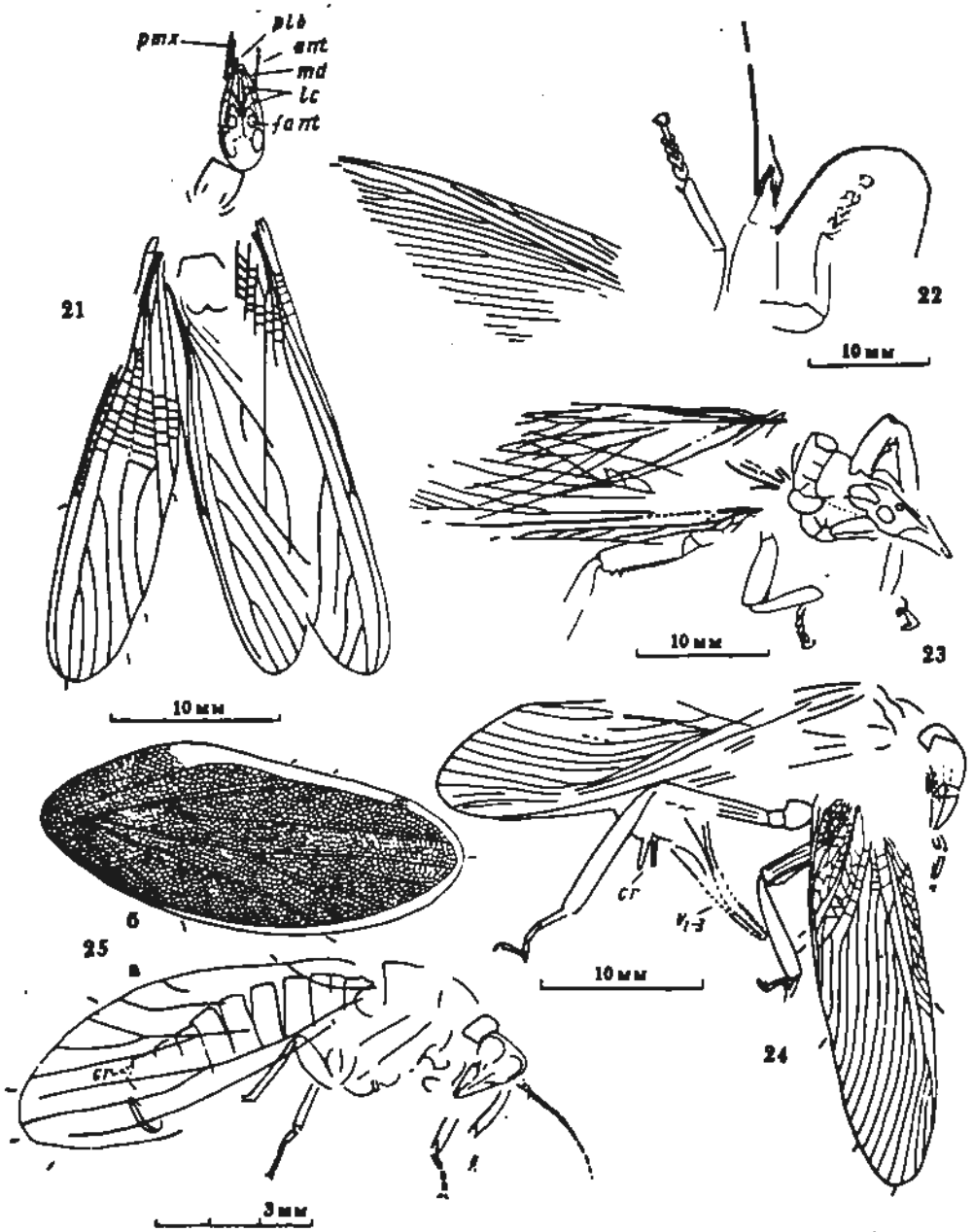
* Parmarrhaphus venosus Martynov from the Late Permian on the Kama river was described as an elytron of a beetle (Martynov, 1930); later on A.G. Sharov discovered that it was simply a torn out clavus (the anal region of the anterior wing) of an insect similar to Strephoneura Martynov. Unfortunately these date never appeared in print.

regarded as an analogue of the depressed MP in Protorrhynchota. The anterior branches of M are here neutral, unlike MA of Protorrhynchota; further differentiation of the rami of the media into a prominent MA and a depressed MP occurs in the Late Permian Homoeodictyidae (plate II, fig. 6). The systematic position of these insects is not clear, but it cannot be ruled out that they are close to Synomaloptilidae and Permarrhaphidae.

Figs. 21-25



Representatives of the order Hypoperlida from the Lower Permian of the sub-Ural region, of the families Synomaloptilidae (21-23), Permarrhaphidae (24) and Perielytridae (25).

21-Synomaloptila longipennis Mart.; 2-Rhinomaloptila polyneura A. Rasn.; 23-Mycteroptila dina A. Rasn.; 24-Strephoneura robusta Mart.; 25-Perielytron mirabile G. Zal.: a-body and posterior wing; b-anterior wing (21-23 from Rasnitsyn, 1977a, 24-25a-originals, composite drawings of the following specimens: 24 ---168/12, 1700/3375, 3376; 25a ---1700/1863, 1864, 4656; 25b ---from Rohdendorf et al., 1962).

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Permarrhaphidae have another characteristic in which they are close to Palaeodictyopteroidea, i.e. the presence of not very long, but distinctly segmented cerci. These cerci could have easily been precursor of the long caudal setae (filaments) characteristic of Palaeodictyopteroidea (figs 26-27). It may be mentioned here that, unlike the males of Palaeodictyoptera and Megasceoptera, the males of Diaphanopterodea may have lacked the caudal filaments that are splendidly developed in their females. At least this is what we have consistently observed among the vast materials on the Early Permian Diaphanopterodea from the collections of the AN SSSR* Paleontological Institute. As was mentioned earlier, the cerci of Hypoperlidae are short and comprise one single segment.

As was already mentioned, it is impossible to derive Protorrhynchota from Synomaloptilidae because of the late appearance of the latter in the geological record. This is equally true of Permarrhaphidae that are known only from the Early and Late Permian of the sub-Ural and Kama regions. The chronological hiatus between the Early Permian and the time when Palaeodictyoptera appear (Early Namurian), is partly filled by the family Strephocladidae that is very similar to them in venation of the wings [other

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* USSR Academy of Sciences. Translator.

parts of their body are not known, but the structure of the head in the close family Tococladidae appears to have been similar to that of Permarrhaphidae (see Carpenter, 1976)]. Apart from the finds mentioned in the literature (in the Late Carboniferous of the FRG and in the Early Permian of the CzSSR and USA, see Carpenter, 1966), there have also been found (but not yet described) forms of Strephocladidae in the Late Carboniferous of Brazil ("Narkemidae sp. C.", Pinto, 1972) and in the Late Permian of the Arkhangel'sk region (the data of the author). Even if we take into account these forms, the chronological hiatus remains rather sizeable: it encompasses the Namurian and the Middle Carboniferous. In the record of that interval there is, however, a considerable number of forms of an indeterminate systematic position that have been referred to Palaeodictyopteroidea entirely on the basis of their wing structure. Given the diversity of venation patterns in Synamaloptilidae, Permarrhaphidae and Strephocladidae, it is quite possible that in the event of more complete remains being discovered, some of the already known Namurian and Middle Carboniferous insects will prove to be representatives of the group of the order Hypoperlida, which we tentatively regard here as the group ancestral to Palaeodictyopteroidea.

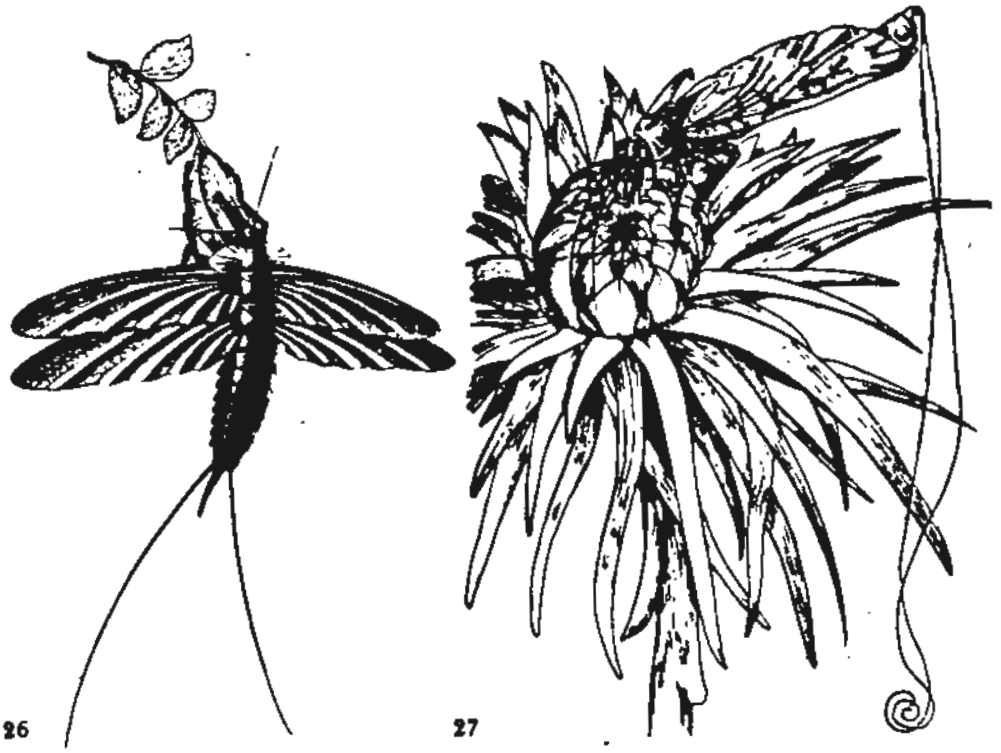
The families Hypoperlidae, Protoprosbolidae, Synomaloptilidae, Permarrhaphidae, Strephocladidae, Tococladidae, Nugonioneuridae and Perielytridae (fig. 25), which were set apart earlier as a separate order under the name of Parielytrodea (Zalesskii, 1948), are thus included with a greater or lesser degree of confidence into the order Hypoperlida. The taxonomic position of Homoeodictyidae, Mixotermitodea, Hapalopteridae, Aenigmatodes and other forms discussed above appears to be less certain.

In addition to Hypoperlidae, Paraneoptera and Protorrhynchota, we are compelled to refer to the cohort Cimiciformes the order Blattinopseida which comprises one single family Blattinopseidae. Blattinopseida (figs 28-29) were always treated as part of Gryllones (=Polyneoptera) within the orders Protoblattodea and Protorthoptera. A.G. Sharov (1968) alone insisted on the need to revise their systematic position.

Blattinopseida occur from the Middle Carboniferous to the end of the Permian. Their body and wing structure has been studied on the basis of a vast collection of the genus Glaphirophlebia from deposits of the Lower Permian age in the sub-Ural region and from the Upper Permian deposits of the Arkhangel'sk region. It has been determined that we are undoubtedly dealing with Scarabaeones that are close with regard to their morphology to Cimiciformes and Scarabaeiformes, but, not being subject to complete metamorphosis, definitely do not belong to the latter (see Laurentiaux, 1959). Blattinopseidae had cryptosterna, a sectorial ovipositor with a protective case and fairly short segmented cerci. Mouthparts of the gnawing kind and not elongated. Structure of laciniae unknown. Folding of wings roof-like; anterior wings often perceptibly reinforced (thickened); a portion of the anal region in the hind wings (posteriorly of the two first anal veins that are the thickest ones) was not only gently expanded, but curled under when the wings were folded, as in Homoptera Auchenorrhyncha, Hemiptera, and in many insects with complete metamorphosis (particularly in beetles and in Hymenoptera). The differences in the structure of RS and CuA in the anterior and posterior wings, respectively, are the same as in Hypoperlida. p.31

Venation varied widely in detail among the representatives of Blattinopseida, but was invariably similar in appearance and displayed a number of distinctive specializations (the tendency to the sclerotization of the wings, the expansion of the subcostal field, the transition of the branches of M to RS, and the expansion and differentiation of the anal region of the posterior wing). These specializations are superimposed, however, on a fairly archaic basis, as is evident from the persistance of M_5, from the backwardly oriented comb of the branches of CuA, and from the characteristic heteronomy of the wings with regard to the structure of RS and CuA.

Figs. 26-27



26 27

Reconstruction of Palaeodictyoptera (26) and Diaphanopterodea (27) (original drawing by A.G. Ponomarenko).

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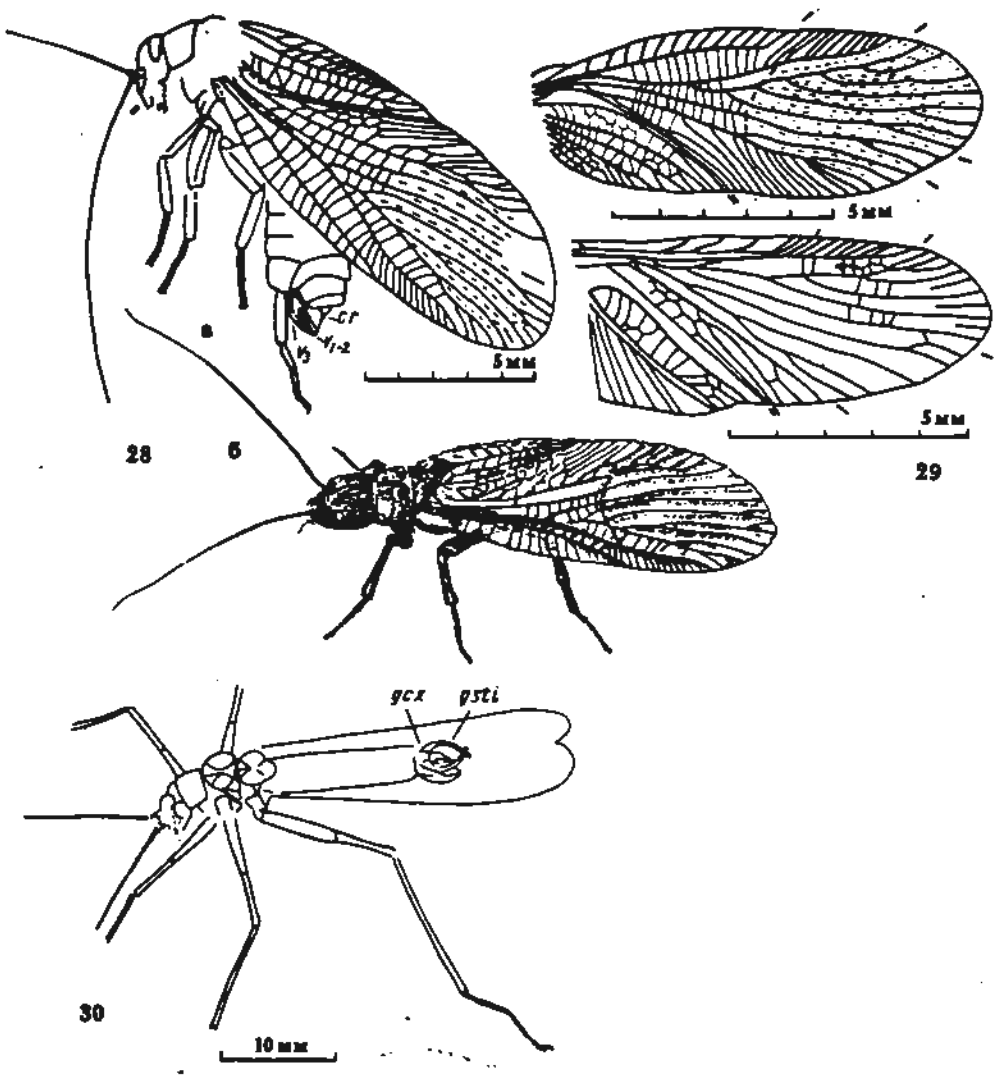
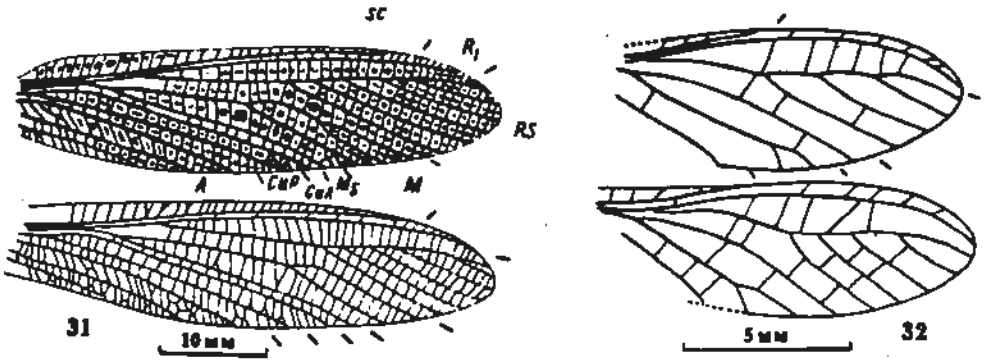
Blattinopseida are highly important in phylogeny because the characteristic features of their body structure correspond to the stage in the evolution of Scarabaeones that may be regarded as the initial stage in the development of both Cimiciformes and Scarabaeiformes (insects with complete metamorphosis). Indeed, they already display cryptosterna, but retain incomplete metamorphosis, segmented cerci, a primitive ovipositor, roof-like folding of the wings and short mandibulae which evidence indirectly that the modifications of their mouthparts along the lines characteristic of Cicimorphes probably had not occurred as yet. Blattinopseida may have also remained similar to their ancestors, i.e. to Protoptera, from the bionomic viewpoint: they may have

continued associating with plants and feeding on their generative organs.

The presence of a vein extending in Blattinopseida along the posterior edge of the anal region in the forewing, may prove to be a highly significant character for determining their phylogenetic links. This vein is characteristic of most Cimiciformes and of many Scarabaeiformes (their more primitive forms in particular), and it plays a certain role in holding in place the wings in repose (perhaps less in the mechanical fixation of the wings than in controlling their position). The posterior edge of the forewing at rest is placed on the sides running from the scutellum of the mesonotum farther back onto the surface of the metanotum; initially it extends more or less along the boundary of the scutum with the prescutum and scutellum.

Figs. 28-32





Representatives of the superorder Caloneuroidea, orders Blattinopseida (28-29), Caloneurodea (30-31) and family Sypharopteridae of an indeterminate position (32).

28- Glaphirophlebia uralensis (Mart.); Lower Permian, sub-Ural region; a-general view; b-reconstruction; 29-G. subcostalis (Mart.); Upper Permian, Eastern Europe; wings; 30-Paleuthygramma tenuicornis Mart.; Lower Permian, sub-Ural region; 31-Caloneura Dawsoni Brongn.; Upper Carboniferous, France; 32-Sypharoptera pneuma Handl.; Middle Carboniferous, USA (28a- the original from Chekarda, specimen PIN N° 1700/3361, wings after the holotype; 28b-original drawing by A.G. Ponomarenko; 29-the original from Soyana, specimen N° 3353/199, 203; 30-the original from Chekarda, specimen PIN N° 1700/1437; 31-from Carpenter, 1961; 32-from Carpenter, 1967).

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In Psocoptera and in many Scarabaeiformes, including probably the Miomoptera, there forms here a broad or two narrower subparallel depressions in which this vein is lodged. In Homopteroidea the fixation apparatus is displaced secondarily onto the mesothorax, where there form two deep, but narrow furrows on the sides of the scutellum, into which the corresponding segments of the posterior edge of the fore wings are fitted. In Neuropteroidea, recent Meropeidae (Mecoptera) and lower Hymenoptera there arises, independently of one another, rough areas at the points of contact on the metanotum and on the wing (Riek, 1967; Rasnitsyn, 1969; Hlavac, 1974; Eichele, Villiger, 1974). In Trichoptera the rough margins of the p.33

field are commonly found only on the wings because the fixation occurs here mainly between the anterior wings overlapping with their posterior margins, in the area cleared of the anal veins issuing into the margins of the wing (an adaptation to the emergence from the pupa in water; Sukacheva, 1976). The metanotum does not, however, cease completely to participate in the fixation of the wings, since its middle portion remains depressed and is commonly bounded by distinct elevations; there may also be observed here structures resembling the rough fields (areas), but they are very weakly developed. The vein bounding the base of the posterior margin in the fore wing disappears in Hymenoptera and Trichoptera (as well as in Lepidoptera), probably as a result of the modifications described above.

The rough fields of Neuroptera have often been ascribed a stridulatory function (Riek, l.c.; Eichele, Villiger, l.c.). This appears unlikely, first of all because these formations are extremely widespread and display no dimorphism in their structure, as well as because their structure (fields bearing spinules or setae oriented towards one another) is not of the type characteristic of stridulatory organs. But even if it had been demonstrated that the rough fields can, indeed, act as stridulatory organs, it would be doubtful that this was their only function. In any event experiments with unilateral excision of the wing segment bearing the rough field in Chrysopa spp. and Hemerobius spp. have shown that, contrary to the findings of Eichele and Villiger (l.c.), the amputation affected the position of the folded wings. First of all, the posterior margins of the wings closed less tightly; secondly, the fixation of the wing on which the operation was performed, lost its former precision and stability: whereas in the vertical position of the body the wings were arranged at the same level, in the horizontal position the impaired wing sagged somewhat. Excision of other segments of the posterior wing does not affect its position in repose.

In Hymenoptera and in the Mecoptera forms Merope Newm. and Austromerope Kill. (Meropeidae) the rough areas were modified

further with formation of specialized coriaceous lobules. In the lower Hymenoptera these lobules, referred to as cenchri, appeared on the metanotum. In Meropeidae (only in their recent representatives, but it should be kept in mind that the Triassic forms differ from them also in many other characters and may have been classified with this family erroneously by Ponomarenko and Rasnitsyn, 1974) they appear on the posterior margin of the wing. In the former instance the exterior of the lobules became squamose and in the latter case it became costate, similarly to the surface of the rough field on the metanotum (Hlavac, 1974).

Among the Gryllones only the groups most specialized with regard to the sclerotization of their wings (such as cockroaches, Dermaptera and brachycerous Orthoptera) use the posterobasal margin of the anterior wing for fixation. Moreover, because of the larger area of overlap of the wings, the edge of the wing that is held in place, is inserted into a depression on the mesonotum rather than metanotum. Groups such as Plecoptera, Mantidae and termites (including Mastotermitidae) have no fixation apparatus of this kind. This suggests that the manner of fixing folded wings that is characteristic of Gryllones and is partly similar to that observed in Cimiciformes and Scarabaeiformes, developed in Gryllones independently of the latter groups (and probably repeatedly), and that the similarity of Cimiciformes and Scarabaeiformes with regard to this characteristic may have been inherited from their common ancestor.

This does not, of course, mean that Blattinopseidae with their specialized venation may have been ancestors of Cimiciformes or Scarabaeiformes. However, we are not discussing that family, but a larger grouping, other members of which may turn out to be p.34
primitive also with regard to their venation. Admittedly, there is little hope that we shall identify them in the collections available, even though they may well be present in these collections. Insects of this kind can probably be identified only from series of well-preserved body remains, a difficult prerequisite to meet when dealing with Carboniferous insects that are the most promising group in this case. We can merely note here that in the

Middle Carboniferous Glaphyrocoris Richardson and Late Carboniferous "Blattinopsis" of the subgenus Stephanopsis Kukalova that have bee described as members of Blattinopseida, as well as in the Middle Carboniferous Protoblattinopseidae, the venation is more primitive, yet has certain features of similarity with that of typical Blattinopseida. They may, indeed, be primitive representatives of the same order.

As was mentioned earlier, there is no evidence that the laciniae of Blattinopseida were split in the manner characteristic of Cimiciformes. Introduction of Blattinopseida into that cohort would deprive Cimiciformes of their only synapomorphy and may appear to be artificial and arbitrary. But given the little knowledge available at this time with regard to Blattinopseida, their classification as a separate cohort seems to be even more controversial. We are therefore compelled to opt for the former of the two solutions open to us, and refer Blattinopseida to Cimiciformes as a separate superorder of that cohort.

Another Paleozoic group that occupies a position similar to that of Blattinopseida and of the forms considered to be close to them near the origins of Cimiciformes and Scarabaeiformes, is the order Caluneurodea (figs 30-31) known from the Middle Carboniferous (the family Genopterygidae) to the end of the Permian. Caloneurodea are characterized by relatively long wings that bear a superficial resemblance to the wings of Synomaloptila (on account of which the latter were described among Caloneurodea; see Martynov, 1938), but are completely homonomous; they also display a characteristic tendency of forming a pair of closely spaced veins in the middle portion of the wing and have densely arranged cross veins. The wings of Carboniferous Caloneurodea (Caloneura Brongniart and Stenarocera Brongniart) folded in the roof-like fashion, while those of the Permian forms folded flatly. Head and mouth parts short; no rod-shaped laciniae of the kind recorded in Blattinopseida have been found; the laciniae may retain their primitive structure. Thorax with a cryptosternum; genitals of both sexes corresponding to the morphological level of Cimiciformes. From the ecological viewpoint Caloneurodea appear to have been a life form of Phasmides to which they are similar

not only in the general habit and proportions of the limbs, but also in the disposition of the cross veins in the wings and in the structure of their eggs. In an impression of a female specimen of Paleuthygramma tenuicorne Mart. from the Lower Permian deposits of the sub-Ural region there have been recorded in the abdomen nineteen large, rigid eggs reinforced by transverse thickenings (plate III, fig. 7). Of course, the similarity of these insects to Phasmides is far from complete. Judging from their ovipositor, which is abbreviated and somewhat reduced, but is nevertheless considerably better developed than that of Phasmides, and from the small number of their eggs, Caloneurodea did not drop their eggs onto the ground, but may have attached them to the surface of plants or hidden them in crevices in the bark, in axils of leaves, or in the incisions which they made with their ovipositor in plants. The absence of reliable references to phylophagy of these and other Paleozoic insects* suggests that they fed on generative parts of plants, similarly to many insects contemporaneous with them, rather than on leaves, as was the case with Phasmides.

Caloneuroidea were treated as part of Polyneoptera until Sharov (1966b) referred them to Oligoneoptera and included them into Neuropteroidea together with Glosselytrodea. If the Glosselytrodea are, indeed, linked by a relatively smooth transition with Neuroptera (see farther on), then we have no evidence that the order discussed is close to insects with complete metamorphosis. Sharov has convincingly demonstrated that Caloneuroidea do not belong to Polyneuroptera (there has never been any doubt that they are neither Palaeoptera, nor Paraneoptera). This does not prove, however, that they belong to Oligoneoptera (i.e. Scarabaeiformes). As long as no definite features of similarity p.35

* There have been reported finds of Paleozoic plants with leaves bearing traces of gnawing (Plumstead, 1963), but there is no evidence that the leaves were gnawed by insects rather than by Diplopoda.

with the latter have been detected in this highly specialized and ancient (more ancient than insects with complete metamorphosis) group, Caloneuroidea should be treated as part of primitive Cimiciformes. Caloneuroidea exhibit no sign of modifications in their mouthparts along the lines characteristic of Hypoperlida and their probable descendants. This permits us to derive Caloneuroidea from the hypothetical group of primitive Cimiciformes which gave rise to the higher typical representatives of the cohort, as well as to Blattinopseida, and to unite them with the latter within the superorder Caloneuroidea. An additional argument in support of the very early divergence of Caloneuroidea is the structure of the medio-cubital region in their wings. As was mentioned earlier, a feature characteristic of the order is the presence of two closely spaced veins in the middle portion of the wing. The anterior one of the two veins is prominent, while the posterior one is depressed. It might appear that we should be able to homologize them on this basis with CuA and CuP, respectively. However, behind these two veins there is yet another depressed (deeply inbedded) vein uniting at the base with the preceding vein, and only the next vein after that has a prominent position (all this is clearly observable even in the wings of Genopterygidae, the oldest Caloneuroidea; see Richardson, 1956, figs 24-25). What we probably see here is M_5 that is free, CuA that is not connected with M_5 and therefore retains its depressed position, as is the case in the posterior wing of Evenkia, and finally CuP that is depressed as usual.

We should mention here the Middle Carboniferous Sypharopteridae (fig. 32) as a group that may be close to Caloneuroidea. Different authors described their phylogenetic relations in entirely different ways, and in the latest work on this group (Carpenter, 1967a) Sypharopteridae are simply classified as insects of an indeterminate systematic position. Venation in the completely homonomous wings of Sypharoptera Handlirsch resembles that of Caloneuroidea, except for the absence of the closely spaced veins that are not always clearly defined even in Caloneuroidea

of the kind of the Permian form Permobiella Tillyard; free M_5 appears to be lacking, but we cannot state this with assurance, since in the only impression available none of the veins posteriorly of the presumed CuP have been preserved. The position of the wings in the impression suggests that the wings were folded in the roof-like fashion.

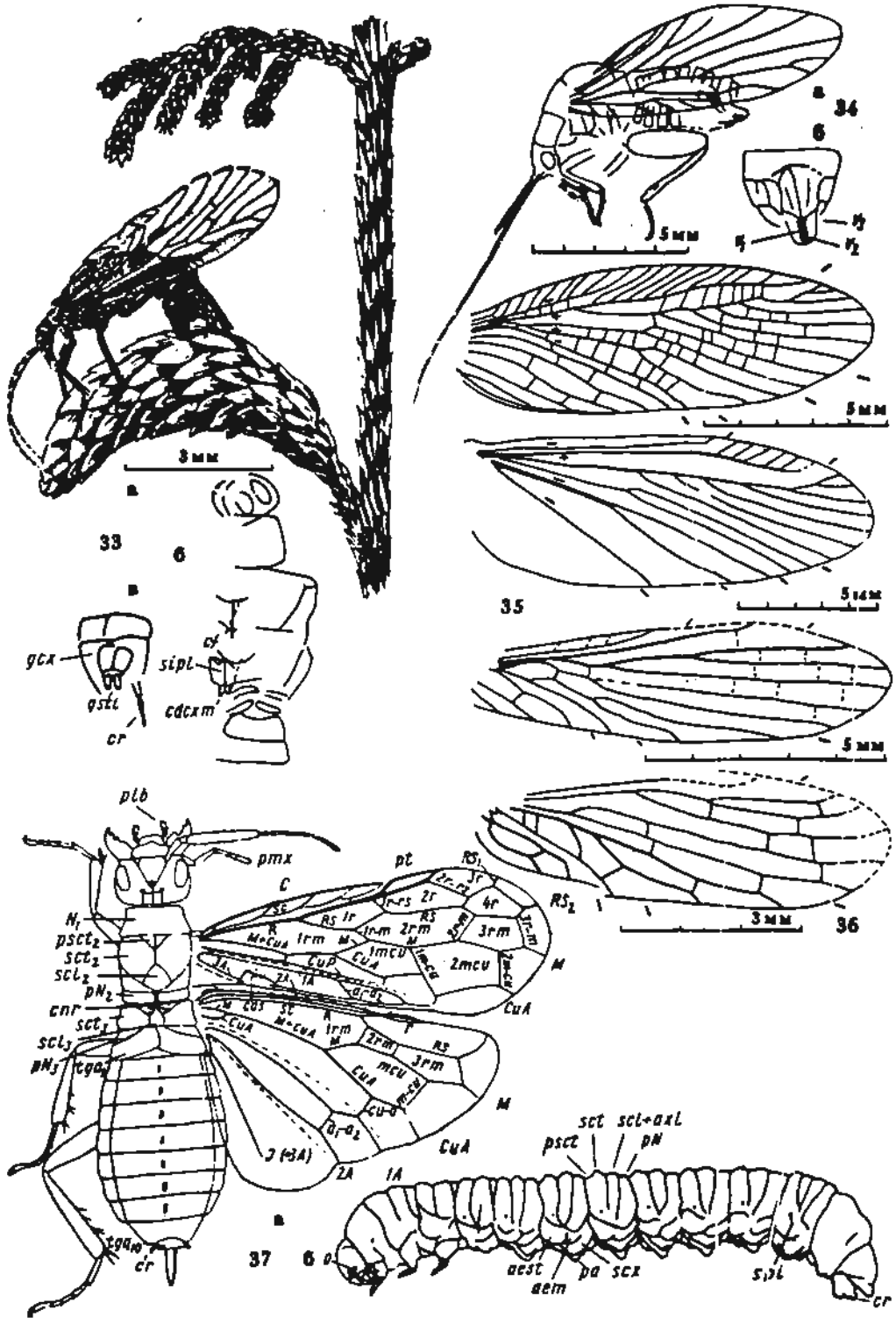
Chapter 4

The structure of Scarabaeiformes and the origin of Hymenoptera

In addition to the well-known assortment of living orders, insects with complete metamorphosis include two extinct orders, Glosselytrodea and Miomoptera. The former was classified in the past with Polyneoptera (Gryllones), but was transferred here and referred to Neuropteroidea by A.G. Sharov (1966b). As was the case with Caloneurodea (see above), A.G. Sharov provided no reliable evidence in support of Glosselytrodea's belonging to Neuropteroidea, but, given the marked similarity in the venation of Glosselutrodea (particularly Permoberothidae) and Neuropteroidea, we can nevertheless agree with Sharov in this decision.

The order Miomoptera (figs 33-36) was transferred from Gryllones to Scarabaeiformes by Rohdendorf (1977), but without substantiating evidence. The size of the order has been changed here from what it was in the other works (Rohdendorf, 1962; Kukalova, 1963; Carpenter, 1967b), and the order includes now insects with the following characters of venation in the wings. RS strictly pectinate, without distinct signs of the branches of M joining it. M biramous, often (particularly in the anterior wing) merging in its basal part with CuA; its anterior branch may be confluent with the posterior branch of RS. CuA biramous, rarely triramous or, very rarely (in some Jurassic Permonkidae), simple. The posterior wing differs from p.37
the anterior wing because its RS and M diverge more proximally (the latter rarely unites here with CuA or unites with it only for a short distance), the trunk of CuA is depressed as far as the bifurcation, the concave fold posteriorly of CuP is less pronounced, and the anal field is somewhat expanded in width relative to that of the anterior wing, rather than in the number of branches of the main vein systems.

Figs. 33-37



Representatives of the order Miomoptera

33-Palaeomantina pentamera A. Rasn.; Lower Permian, sub-Ural region;

a-Reconstruction; b-Structure of the thorax, c-Genitals of a male; 34-Palaeomantisca lata Mart.; Lower Permian, sub-Ural region: a-General view; b-Ovipositor viewed from below; 35-Epimastax sojanensis (A.Rasn.); Upper Permian, Arkhangel'sk region; 36-Perminka jurassica A.Rasn.; Lower Jurassic, Fergana region (33-original drawings by A.G. Ponomarenko; the other drawings from Rasnitsyn, 1977a).

Fig. 37
The hypothetical ancestor of Hymenoptera
a-Imago, b-larva (a-from Rasnitsyn, 1969, b-original).

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Miomoptera are divided here into three families: Palaeomanteidae, Palaeomantiscidae and Permosialidae. The first family includes most representatives of the order and is characterized by the roof-like folding of the wings, a narrow costal field of the somewhat thickened anterior wing, and by the absence or (less often) a small number of the preapical branches of SC. Palaeomandeidae are known since the Late Carboniferous and are both very varied and widely distributed in the Permian. The somewhat sketchily described Archaemioptera Guthorl may be close to Palaeomanteidae (the form Tychtodelopterum O.Mart. described as part of Archaemiopteridae, belongs to Megaloptera rather than to Miomoptera; Ponomarenko, 1977a). Palaeomantiscidae are known only from the Early Permian of the sub-Ural region (Rasnitsyn, 1977a). They are close to Palaeomanteidae, but differ from them in having more markedly membranaceous anterior wings and saltatorial posterior limbs. Palaeomantina A. Rasn., one of the two genera of this family, has five-segmented tarsi (in the type genus and in Palaeomanteidae the tarsus has four segments, and the tarsus of Permosialidae is not known).

Permosialidae are composed of five genera: Permosialis Mart., Epimastax Mart. (=Sindomioptera A.Rasn., syn.nov.), Permonka Riek, Permonia Kukalova and Permonikia Kukalova. They are characterized by the flat folding of the wings (known only

for Permonka) and by a broad costal area (field) of the anterior wing with profusedly ramified SC. The family is known from the beginning of the Permian and until the Early or Middle Jurassic. Moreover, most of the genera are Permian and the only genus known from the Mesozoic is Permonka, if we disregard the single find of Permosialis sp. in the Triassic of Central Asia (Dzhailoucho). The data evidencing that Permosialidae belong to Miomoptera rather than to Megaloptera have been presented by Riek (1976) and Rasnitsyn (1977a). In the latter work the author introduced into this family the genus Epimastax (under the name of Sindomioptera) and instituted the family Permonkidae. However, Riek's suggestion (1.c.) to include Permonka into Permosialidae appears to be better substantiated. Permonia and Permonikia were described as part of the family Permembiidae (Kukalova, 1963), but Permembia Tillyard turned out to be a representative of Gryllones (Carpenter, 1976). Permonia has already been referred to Permosialidae by Riek (1.c.) and Permonikia should probably be also classified with that family.

As was mentioned earlier, until now Miomoptera were referred to Polyneoptera (Gryllones). Even their nymphs were described (Sharov, 1957). Analyses of the type material show, however, that these nymphs differ insubstantially from those of Protoblattodea. In any event they do not belong to Miomoptera: the posterior wing cases of these nymphs are markedly expanded at the base which suggests the presence of a broad anal region in adult individuals, whereas in Miomoptera the base of the posterior wing is only slightly expanded.

Another character that served as a criterion for referring Miomoptera to Gryllones is the presence of short segmented cerci (Carpenter, 1939). The presence of such cerci in lower Scarabaeiformes is, however, quite natural, particularly since three-segmented cerci are found in females of Mecoptera (Mickoleit, 1975). It is considerably more significant that Miomoptera have features characteristic of Scarabaeones. We are referring to the roof-like folding of the wings in their oldest and most primitive families Palaeomanteidae and Palaeomantiscidae; the anal region

of the posterior wing that does not curl under, when the wing folds down, even if it is slightly expanded; the cryptosterna; the sectorial ovipositor with the third valves forming a protective case; and the symmetric genitals in males, whose gonocoxae and gonostyles form the grasping apparatus. We know only one morphological characteristic of the imago specific of Scarabaeiformes (the additional median joint of pterothoracic coxae).* This character has also been found in Miomoptera (see fig. 33b), which permits us to refer them to insects with complete metamorphosis. p.38

From the viewpoint of morphology of the imago Miomoptera are primitive enough to be ancestors of all the other Scarabaeiformes, particularly since there are no other known candidates for that role among the insects with complete metamorphosis that are comparable to them in the level of primitiveness. The presence of a mere two-three branches in M can scarcely be regarded as a serious obstacle to deriving the other Scarabaeiformes from Miomoptera, since the polymerization of venation is a fairly wide-spread phenomenon (it has been demonstrated by Carpenter, 1939, for Odonata and by Ponomarenko and Rasnitsyn, 1974 for Protomecoptera; a virtually identical process occurred in the evolution of Neuroptera, of Megaloptera from the family Corydalidae, of many Jugatae from the superfamily Fulgoroidea, etc.). Nor does the expanded base of the posterior wing rule out the presumed phylogenetic role of Miomoptera, since the narrow base of the posterior wing in Neuropteroidea proportional to their light and slender body, may be a secondary character. In any event the cubito-anal region of the wing in the Permian Permithonopsis grandis O.Mart. exhibits all the major characteristics of the posterior wing of Miomoptera (Martynova, 1952, fig. 13), as is also the case in some (if not all) of the Permian Neuroptera.

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* Median joint of the coxae is also known in Ephemeroptera (Rasnitsyn, 1969).

The geological range of Miomoptera encompasses the whole period during which the principal phylogenetic branches of Scarabaeiformes appeared. The order arose no later than the beginning of the Late Carboniferous, i.e. earlier than any of the other representatives of the cohort (Mecopteroida, Neuropteroida and Coleoptera are known only since the Early Permian) and became extinct during the Jurassic after Hymenoptera made their appearance in the Triassic. These are the data leading us to believe that Miomoptera could have been the group ancestral to all the other insects with complete metamorphosis.

We have not succeeded in finding a smooth transition from Miomoptera to any of the superorders of insects with complete metamorphosis. Therefore Miomoptera should probably be regarded as a separate superorder designated as Miomopteroidea.

The structure of Miomoptera provides relatively little material for reconstruction of their ecology. The roof-like folding of their wings and their long limbs testify to a predominantly open mode of existence, probably on plants. However, judging from the somewhat thickened anterior wings in most of their representatives and from the tendency, realized in Permosialidae, to fold the wings flatly, many Miomoptera were capable of penetrating into narrow spaces (to hide in crevices in the substratum or perhaps to squeeze into the strobiles of gymnospermous plants in search of food). There is no direct evidence that Miomoptera imagos fed on pollen, but it is supported indirectly by the wide-spread pollinophagy among their probable descendants, i.e. among the other Scarabaeiformes (Grinfel'd, 1962). The consumption of pollen by living insects may, of course, be regarded as a consequence of the spread of gymnospermous plants, but many Paleozoic and Mesozoic forms also appear to have been pollinophagous. The Jurassic Kalligrammatidae that were thickly pubescent and resembled superficially brightly coloured butterflies with oculiform pterostigmas, were almost definitely anthophiles. Moreover, at least Meioneurites villosus Panf. had elongated villous palps forming, when folded, a proboscis-like structure (Rohdendorf, 1969, fig. 17). The insect may have used

this "proboscis" for extracting pollen from the generative organs of gymnosperms. Structurally and, probably, functionally similar palps have been detected in one of the oldest forms of Mecopteroidea (Marimerobius G.Zal.; plate III, fig. 8). According to the data of Sukacheva (1976), this insect belongs to Trichoptera.

Palaeomantiscidae with their narrow and equally thin membranous anterior and posterior wings and saltatorial hind limbs were probably less inclined to hide in sheltered places than the other Miomoptera may be presumed to have done.

The similarity of the mode of life of some of the descendants of Miomoptera (Xyela Dalm., Hymenoptera) to that presumed for primitive Pterygota, as well as the structure of their ovipositor adapted to laying eggs in plants, suggest that the larvae of Miomoptera developed in more or less mature cones of gymnospermous plants moving inbetween the scales from one microsporangium to another. This hypothesis also permits us to explain a number of features characteristic of complete metamorphosis. Larvae of the insects undergoing complete metamorphosis differ from the preimaginal phases of the other winged insects (most of all from the nymphs of Gryllones) in having characters testifying to the weakening of the locomotory and sensory functions (decrease in the relative measurements and reduced segmentation of the limbs; loss of well-defined boundaries between the thoracic tagma, and a certain reduction of the eyes and antennae). These characters may have evolved as a result of a relatively immobile mode of life under sheltered conditions that effectively protected the insects against dehydration, enemies, etc., and in the presence of an abundant food supply. The delay in the development of the laterally projecting wing cases may denote the primary existence of the larvae in cramped spaces.* The conditions of development inferred for Miomoptera meet all these requirements.

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* The inhibited development of external genitals in larvae of the insects with complete metamorphosis may have been a side-effect of the modifications listed above, since it proved possible to induce them by simply arresting the morphogenesis at the phase preceding the stage of young larvae of Ephemeroptera (without ocelli and with an undifferentiated tibiotarsus) which obviously have no external rudiments of genitals. These types of mechanisms of evolutionary changes are examined in greater detail by A.L. Tikhomirov (1976).

In addition to the distinctive structural characters of the larvae, complete metamorphosis is identified by the presence of a pupal stage that involves not only profound differences, but also a sharp transition from the larval to the imaginal mode of existence. The development of Miomoptera in strobiles of gymnospermous plants also satisfies this prerequisite. p.40

Miomoptera are similar to Hypoperlida in their general habit and in the venation of their wings. This resemblance is particularly pronounced in Palaeomantiscidae (see fig. 33). It is nevertheless difficult to derive them from this group or from its immediate ancestors (more primitive Hypoperlida of the type of protoprosbolids), since the presence of a stylet-like lacinia in their descendants (i.e. Paraneoptera), as well as in Sinomaloptilids that are close to them, and possibly even in Miomoptera themselves strongly suggests that this character already developed in primitive Hypoperlida. The lower Scarabaeiformes to which the Miomoptera belong, had no specialization of this kind, since it is lacking in most insects with complete metamorphosis (even though in Scarabaeiforms there are some preconditions for the division of the lacinia, as is evident from the data presented by Kristensen, 1975). On the other hand Miomoptera resemble in some of their characters Blattinopseidae (a more robust body than that of Hypoperlida, a somewhat expanded base of the hind posterior wing and the characteristic aspect of the wings in Epimastax Martynov from the family Permosialidae). If not Blattinopseidae themselves, then some other representatives of the order Blattinopseida or, in the extreme case, of the superorder Caloneuroidea were primitive enough to give rise to Miomoptera, hence to all the insects with complete metamorphosis.

The descendants of Miomoptera split up into two separate groups, one of which includes Hymenoptera, while the other one comprises Coleoptera, neuropteroids, and mecopteroids. The repeatedly voiced hypothesis that Hymenoptera are close to mecopteroids appears to be groundless. The latest papers dealing with this problem (Kristensen, 1975; Konigsmann, 1976) list three synapomorphic characters of Hymenoptera and Mecopteroida.

All of them are characteristic of larvae and are as follows: the eruciform (worm-like) body shape, the presence of one single unguis, and the secretion of silk by the labial glands (in Neuropteroida and Coleoptera the primary shape of the larval body is campodeiform, the ungues are paired, and silk is secreted by the malpighian tubes). However, the apomorphic* nature of these characteristics is questionable. Unguiform praetarsus precedes paired ungues ontogenetically and phylogenetically (polypods in the broad sense, bristle-tails, Monura in particular, and May-flies) and the ungues may form independently, even in Hymenoptera (Argidae: Rasnitsyn, 1969). The eruciform shape of the body is better suited to the mode of existence presumed for the larvae of Miomoptera than a campodeiform body, and there is no evidence suggesting that it is a secondary development. As concerns the p.40
secretion of silk, the change-over from the labial to the malpighian secretion has been established with confidence (in Hymenoptera; Gilmour, 1970), but not the other way around. Furthermore, in primitive Mecopteroida, i.e. in Mecoptera, there has so far been found no secretion of silk at all.

The appearance of the group uniting Coleoptera, Neuropteroida and Mecopteroida may have been related to the change-over to the development in plant remains and their concentrations (ground cover, decaying wood, empty spaces underneath the tree bark, etc.), which is reflected in the structure of their head capsule and ovipositor. Prognathism, at least functional (facultative), if not organic prognathism, resulted in the closure of the head capsule (between the oral opening and the occipital foramen) that is extremely characteristic of both the larvae and the imagos in the three superorders of this group. Open head capsules are found very rarely. Even though it may be assumed that in some instances (e.g. in beetles of the family Cupedidae) the open head capsule was inherited directly from the ancestral forms, it may be a secondary character developed as a result of a partial juvenilization of the larva (persistance in the larva of the features characteristic of the late embryo).

* =apomorphous. Translator.

With the change-over of the larvae to a different habitat and appropriate modifications in the mode of oviposition (in crevices in the substratum instead of in living plant tissues) the differentiation of the valves of the ovipositor into the sectorial (the first and the second pairs) and protective types (the third pair forming the case of the ovipositor) became superfluous. As a result of this the third pair of valves began to actively penetrate into the substratum and became a functional part of the ovipositor, while their second pair became unnecessary and was reduced. There may often be observed a subsequent reduction of the first pair of valves followed eventually by the complete disappearance of the ovipositor.

The structure of the larval eyes specific of the group discussed may also be related in some way to the new habitat of the larvae. We are referring to the division of the compound eye into ommatidia and their regrouping into the rosettes consisting primarily of six units. A cardinally different structure can probably be found only in the larvae of Mecoptera which have true compound eyes (in Panorpidae) in addition to a structure resembling closely the median frontal ocellus (Riek, 1970a; according to the data of the author, this ocellus is developed only in young larvae of Panorpidae). On the other hand the arrangement of the seven ocelli in Bittacidae closely resembles a rosette, and the three ocelli in Boreidae suggest its rudiment. It may therefore be assumed that the compound eye of the Panorpidae larva is of a secondary nature (i.e. arose as a result of the partial adultization of the larva) and that the presence in the larvae of an ocular rosette or a strong tendency to develop such a rosette is characteristic of the whole branch of Scarabaeiformes discussed. The existence of some preconditions for the formation of the rosette in the development of the compound eye in insects may be inferred from the fact that the eye of most Odonata undergoes a similar state in the process of ontogenesis (Ando, 1957). In addition to paleontological data, studies on larvae of Meropeidae and Notiothaumatidae may provide reliable information pertaining to the history of the six-partite ocular rosette in

Scarabaeiformes.

Apart from the characters described above, Mecopteroida, Neuropteroida and Coleoptera exhibit distinctive features of venation in the wings that have not been found either in Miomoptera, or in Hymenoptera. One of these characters is the multiramous (secondarily ?) M, the anterior portion of which (the whole MA or, rather, its anterior branch) goes over into the RS system, but in doing so, retains its bifurcations. As a result of this RS may appear to be dichotomous (in Coleoptera the migrant branch of MA which joined the RS system, is free of bifurcations, but it may be a secondary development). The base of the M branch that changed over to RS often persists in the wings of Neuropteroida and of some Paleozoic beetles (see Ponomarenko, 1972); in Mecopteroida it has been obliterated, but the less complex nature of their "RS" is often clearly evident (see Ponomarenko, Rasnitsyn, 1974).

Another feature characteristic of venation in the three superorders examined is the loss of the primary structure of CuP in their posterior wings. The primitive state of the cubital system similar to that in Miomoptera (both CuA and CuP are depressed, the former bearing a distal bifurcation, the latter simple and independent of the anal system), persist only in some Permian Neuroptera of the kind of Permithonopsis grandis O. Mart. In some of the living Neuroptera CuP has also a concave position, p.41
but either CuP itself, or the common trunk Cu is connected at the base with A_1 by a cross vein (Megalomus spp., Drepanopteryx spp. and Sisyra spp.). In other cases CuP is neutral or even prominent and may be either connected in some manner to A_1, or be independent of it, but, (judging from its position in the membrane) the lack of a link with A_1 is then a secondary phenomenon; in some cases CuP was simply lost (some Hemerobiidae).

The divergence of the second evolutionary stem of Scarabaeiformes represented by Hymenoptera, does not appear to have altered significantly the mode of existence of their larvae: the larvae continued developing in male cones of gymnosperms feeding

on their pollen. The larvae underwent some morphological modifications (the distinctive manner of reducing the compound eyes by way of uniting basal structures underneath a common lens instead of breaking up into ommatidia), but the most intensive evolutionary changes occurred in the structure of adult insects, primarily in the organs and structures associated with flight. The flat or, rather, the overlapping position of the wings in repose that is characteristic of Hymenoptera, appears already in Miomoptera (Permonka). As a result of the changes in the manner of folding the wings the rough areas (fields) of the metanotum on which the corresponding portions of the anterior wing rest in repose, may have been modified in Hymenoptera to more specialized organs responsible for holding the folded wings in place, i.e. to the coriaceous plates referred to as cenchri. The rough fields of the anterior wings co-adapted to them became localized in the region demarcated by the characteristic curvature of the posterior anal veins.

Venation of the wings also underwent considerable changes: it became reduced rather than polymerized, as was the case in the other Scarabaeiformes (RS was reduced to two branches, M and CuA to one single branch, and CuP disappeared almost completely). The position of most of the veins in the membrane became practically neutral, except for the markedly depressed SC of the forewing and the prominent (relative to SC) C and R. Furthermore, there appeared sharp flexures in the veins, the segment in which M and CuA are confluent, increased in length, and the tendency of RS and M to unite became apparent; the posterior part of the anal region in the hind wing, including the third anal vein, expanded even more markedly than that of Miomoptera and began to curl under during the folding of the wings. The expansion and folding under of that region (to which we refer here as the jugal region) may be related to the modification of the body shape, which became shorter and heavier, and to the shortening of the wings, of the posterior wings in particular.

However, the most significant modifications in the flying apparatus were those involved in the change-over to the functionally dipterous flight. There developed means of securely fastening the wings over a considerable portion of their line of contact in the form of three groups of uncinate setae on the hind wing hooking onto the folded-under posterior margin of the forewing. The posterior wings decreased in size and became triangular as a result of the expansion of their anal region: the venation of the wings grew simpler. Parallel to that there occurred a significant reduction of the metathorax and hypertrophy of the mesothorax. Moreover, mesothoracic muscles were strengthened at the initial stages in the evolution of the order at the expense of the horizontal muscles of the wing, a process accompanied by the expansion of the anepisterna bearing these muscles, at the expense of the praepisterna; the vertical muscles assumed the principal role at a later stage (Rasnitsyn, 1969).

A number of the characters evolved appear to be unrelated to the improvement of flight. One of such characteristics is the thickening and confluence of the basal segments in the flagellum of the antennae forming in many primitive groups a long and thick composite segment with segmented flagellum itself diverging off the tip. The functional significance of this adaptation is not clear. An ideal cleaning mechanism formed by the spur of the anterior tibia and the first segment of the tarsus, may have evolved in response to the intensification of imaginal feeding on pollen (Grinfel'd, 1962). The splitting up of the first abdominal tergite that is characteristic of Hymenoptera (and is another modification, the functional meaning of which is obscure), may turn out to be a character acquired by the ancestors of the insects examined, since we cannot rule out its possible presence in Miomoptera (see fig. 33b).

Another important acquisition of Hymenoptera, which had a marked effect on their further evolution, was a distinctive mechanism of sex determination, i.e. a haplodiploid population system with fertilized eggs developing into diploid females and unfertilized eggs into haploid males (a form of parthenogenesis referred to as arrhenotoky). The haploidy of the males had a

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number of evolutionary consequences. First of all, all the alleles of the haploid male are in the hemizygous state equivalent to the homozygous state of diploid individuals, and fully exercize their effect on the selective properties of the individual (excepting naturally those aspects of their activity that are the prerogative of the females). As a result of this any selectively positive alleles appearing regularly in a haploid individual, will rapidly spread within the population, regardless of whether they are dominant or recessive, while selectively negative alleles will be just as rapidly eliminated. As a result of this the gene pool of the population will become markedly impoverished on account of the hidden reserve of variability (excluding the alleles that are effective only in females), as a consequence of which the resistance of the population to inbreeding will increase (Rasnitsyn, 1969; Lin, Michener, 1972; Gershenzon, 1974). The reduction of the genetic polymorphism of the population had no observable negative effect either on the adaptability (the level of the biological progress attained) or on the rate of evolution of Hymenoptera, which are one of the richest groups of insects with regard to its species diversity, as well as one of the biocoenotically most important and rapidly evolving groups. It cannot be ruled out that the increased genetic uniformity of the populations is compensated here by a greater diversification of their adaptive behaviour, which appears to be characteristic even of the lower Hymenoptera (Rasnitsyn, 1969). Nor can it be ruled out that these two phenomena are bound by some causative link (the diversity of the adaptive behaviour may have arisen, for example, as a compensation for the impoverishment of the gene pool or, conversely, may have facilitated the transition to the haplodiploid system thus compensating for the reduction of the population polymorphism).

The immunity of Hymenoptera to inbreeding should (at least theoretically) increase the stability of small populations (including those which originated from the same archetype and contribute to the formation of tightly [stable] [knit] colonies of closely related individuals, which is one of the major prerequisites

for the development of sociality in that group.

Another important consequence of the haplodiploid population system is the possibility of arbitrarily determining the sex of the offspring by regulating the supply of the sperm stored in the spermatheca, to the ovum laid. This makes it possible first of all to ensure the optimal conditions for the descendants in the case of the requirements of the developing females and males being different, and, secondly, to reduce, if necessary, the proportion of the males among the progeny.

All the other conditions being equal, the reduction of the percentage of the males increases the reproductive potential of the population and, in addition to it, is among the major prerequisites for the development of sociality in insects with complete metamorphosis.

The haplodiploid system also acts as an automatic mechanism for sustaining the optimal ratio of sexes: in the event of a shortage of males a portion of the females remains unfertilized and lays haploid eggs, as a result of which the number of the males increases in the succeeding generation. Having reached its optimum level, the number of males automatically ceases to increase further (Rasnitsyn, 1969).

Lastly, the haplodiploid system of sex determination entails a distinctive distribution of the levels of genetic similarity among the related individuals. This also appears to have affected markedly the evolution of sociality in Hymenoptera (see more detail in part III, chapter 4).

Hymenoptera appeared no later than in the middle of the Triassic period, since their oldest remains were found in deposits of the Middle or Upper Triassic (Rasnitsyn, 1969; in that work the deposits in question were erroneously dated as Lower Triassic; see Dobruskina 1970, 1974, and Ponomarenko, Rasnitsyn, 1974, for information on their age). The general appearance (habit) of the imago and larva of the hypothetical primitive Hymenoptera is shown in fig. 37. The position of the order in the phylogenetic tree of insects is shown in fig. 5.

PART II

EVOLUTION OF THE LOWER HYMENOPTERA (SUBORDER SYMPHYTA)

Chapter 1
The early stages of the evolution of Symphyta

Evolution of the lower Hymenoptera is discussed in a separate work (Rasnitsyn, 1969). The main conclusions and pertinent additional data are presented in this work. The system of the suborder adopted by us is shown in table 2; see the phylogeny tree in fig. 38. Pg. 89.

As was demonstrated in the work mentioned above, the closest common ancestor of all the Hymenoptera (see fig. 37) should have had the principal characters of Xyelidae and must have belonged to that family. Its larva probably lived in male cones of gymnospermous plants and fed on their pollen, similarly to the living Xyela Dalm., but, unlike the latter, may have associated rather with more or less mature cones that were already open to a greater or lesser degree, since the effect of the endophytic mode of existence (inside plant tissues) on insects is similar to that of parasitism. Therefore the larvae of Xyela (fig. 39) developing in young tightly closed pine cones, or even more so the larvae of some of the other recent Xyelidae living inside shoots of gymnospermous plants, have a markedly reduced morphology. The larvae of Pleroneura Konow are, for example, very similar in habit to the larvae of the lower Hymenoptera gnawing wood, those of Cephidae in particular. Among the living Xyelidae the least markedly reduced larvae are those of Macroxyelini (fig. 40) which changed secondarily to an open mode of life and feed on foliage and buds of angiosperms. Their structure exhibits no fundamental modifications related to the open mode of existence at the final stage of their evolution. Indeed, their habit displays many features in common with the larvae of Panorpa which, as is well known, exist in more or less sheltered situations (burrows in the ground, open spaces in the ground cover, etc.), but may also be encountered outside the

shelters. They have relatively long bristle-like antennae that are similar to those of many larvae leading a sheltered existence (in particular Pamphilioidea, Blasticotomidae, Mecoptera and moths of the suborder Zeugloptera), rather than the shortened antennae of the Tenthredinoidea larvae existing in the open. Macroxyelini also differ from the latter in having weakly developed thoracic and, particularly, abdominal limbs, and resemble more closely in this respect the larvae of Mecoptera and Zeugloptera. Abdominal legs as such are in fact lacking in these larvae: abdominal sternites bear a transverse row of six papillae, among which the lateral ones correspond in topography to the lateral part of the subcoxa (catapleura) of the thoracic segments; the second most strongly developed pair is situated at the level of the thoracic legs; and lastly, the weakest median papillae (or simply tubercles) may correspond to the median part of the thoracic subcoxa. Comparison of this arrangement with the data presented by E.F. Martynova (1950) suggests that whereas the second intermediate pair of papillae corresponds in topography to the abdominal limbs of the Tenthredinoidea and higher Lepidoptera larvae and appears to be homologous with them, the lateral papillae may be juxtaposed with the abdominal legs of the Zeugloptera (Micropterygidae) larvae, and the median papillae with the limbs of the Panorpa larvae.

It is equally significant that the larvae of Macroxyelini have strongly developed sensory subanal tubercles which correspond in function to the segmented subanal appendages found in many larvae of the lower Hymenoptera that exist in sheltered situations (Blasticotomidae, Pamphilioidea or Cephidae; see figs 57 and 58), and appear to be precursors of these appendages. Among the Symphyta living in the open this type of structures is found rarely and only in their more primitive forms (Argidae Stericophorinae, Pergidae Philomastiginae; see fig. 53b). Well-developed tactile organs on the posterior end of the body are generally most characteristic of more or less mobile insects existing in semi-confined situations (in the passages burrowed by other insects, crevices in the substratum, etc.). It would appear that the primary type of larvae of Hymenoptera was fairly similar

in morphology and general habit to the larvae of Macroxyelini, except for the shape of their terminal tergite, which was probably conical, as in Xyelinae (Rasnitsyn, 1977d).

TABLE 2

The system of the lower Hymenoptera (suborder Symphyta) adopted in this work.

Rank of the taxon	Name	Notes
Order	Hymenoptera	
Suborder	Symphyta	
Infraorder	Xyelomorpha	
Superfamily	Xyeloidea	
Family	Xyelidea	
Infraorder	Tenthredinomorpha	
Superfamily	Tenthredinoidea	
Family	Xyelotomidae	
Family	Blasticotomidae	
Family	Electrotomidae	
Family	Argidae	
Family	Pergidae	
Family	Cimbicidae	
Family	Tenthredinidae	Including Diprionidae
Infraorder	Siricomorpha	
Superfamily	Pamphilioidea	
Family	Xyelydidae	
Family	Pamphiliidae	
Family	Parapamphiliidae	
Family	Megalodontidae	
Superfamily	Siricoidea	
Family	Gigasiricidae	
Family	Anaxyelidae	
Family	Xiphydriidae	
Family	Siricidae	Including Sinosiricidae Hong

Family	Sepulcidae	
Family	Pararchexyelidae	
Family	Myrmiciidae	=Pseudosiricidae, probably a composite artificial group
Superfamily	Cephoidea	
Family	Cephidae	

Primitive Hymenoptera may have been very close in morphology to the oldest known representatives of the order, i.e. to Xyelidae of the subfamily Archexyelinae found in the Middle and Upper Triassic deposits of Fergana and in the Upper Triassic from Australia (the larvae of Archexyelinae are unknown).

The phylogeny tree of Xyelidae (Rasnitsyn, 1971c) is composed of two trunks, one of which comprises the subfamily Macroxyelinae (figs. 41), the other one Xyelinae (fig. 42) and Madygellinae (figs 43-44). All the other Symphyta also form two evolutionary lines: one of them, represented by Tenthredinoidea, exhibits a marked resemblance to Macroxyelinae, while the other one comprising Pamphiliodea, Cephoidea and Siricoidea, resembles Xyelinae and, particularly, Madygellinae. Macroxyelinae are, indeed, characterized by the dorsal position of the larval ocelli relative to the antennae, the top of the costal vein joining R, and, most importantly, by the tendency of their larvae to abandon sheltered situations that is evident in Macroxyelini, and to have consequently a shortened ovipositor. The same features are characteristic of Tenthredinoidea. The inverted genitals of Tenthredinoidea do, indeed, form a link with Xyelinae, but this character has also been recorded in Pamphilioidea and Siricoidea; moreover, their genitals, similarly to those of Xyelinae and unlike those of Tenthredinoidea, develop initially in the normal position, then become inverted. Among Siricoidea and Pamphilioidea inverted genitals are rare. Observations on Xerix spectrum L. (Siricidae) have shown that the inversion is there facultative and temporary, whereas in Xyelinae it is permanent and obligate. It cannot be ruled out that the males of Macroxyelinae are capable of inverting

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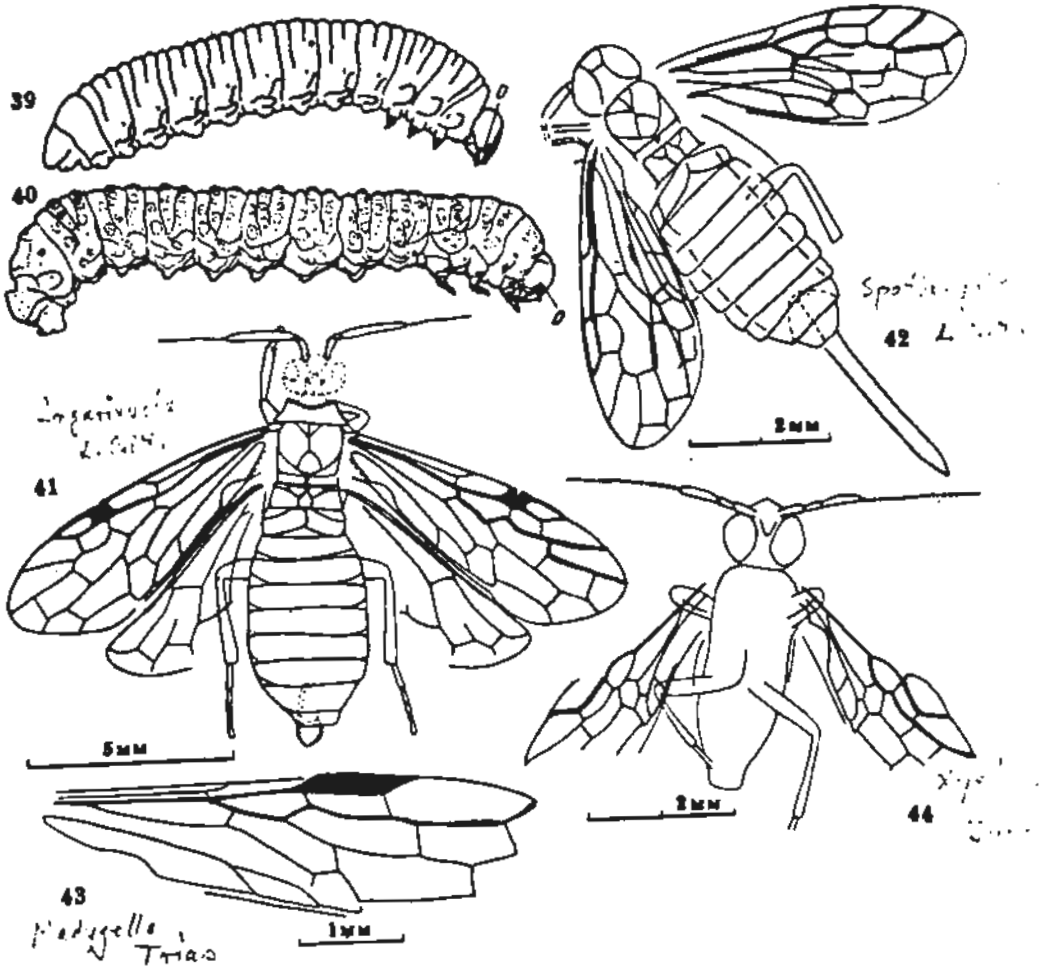
their genitals at least at the time of copulation. The view that the inversion of the genitals developed independently in Tenthredinoidea and Xyelinae is also supported by the normal position of the genitals in Blasticotomidae (Togashi, 1970).

Figs 39-44



Representatives of the family Xyelidae
39-Larva of Xyela sp., recent; 40-Larva of Megaxyela major Cress; recent; 41-Angaridyela vitimica A. Rasn.; Lower Cretaceous, trans-Baykal region; 42-Spathoxyela fossilis (A.Rasn.); Lower Cretaceous, trans- Baykal region; 43-Madygella analoga A.Tasn.; Middle-Upper Triassic, Fergana; 44-Xyelula hybrida A.Rasn.; Upper Jurassic, Southern Kazakhstan (39-from Smith, 1967; 40-from Yuasa, 1923; 41-44--- from Rasnitsyn, 1969).

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The characters uniting the second group of the Lower Hymenoptera (Xyelinae, Madygellinae, Pamphilioidea, Cephoidea and Siricoidea) are first of all their existence in confined situations (in most instances simply in plant tissues) and, in addition to it, the posteroventral position of the ocelli relative to the antennae* in their larvae, the long ovipositor of their females (except for Pamphilioidea, where it is markedly shortened secondarily), and C of the forewing that is not connected apically to R anteriorly of the base of the pterostigma. p.46

It is equally significant that the development of larvae inside the shoots of gymnosperms results in considerably greater modifications along the lines characteristic of Cephoidea and Siricoidea in Xyelinae (Pleroneura) than in the Macroxyelinae larvae (Xyelecia Ross). We should also mention the similarity of Siricoidea and Madygellinae with regard to their venation and, partly, general habit. Madygellinae resemble probably most closely the ancestors of the group Pamphilioidea-Siricoidea or may even be their ancestors. On the other hand they are very close to Xyelidae and, from the viewpoint of morphology, may easily be their descendants. It is true that they appear in the paleontological record in the latter half of the Triassic period, while Xyelini have been recorded only since the beginning of the Jurassic. But the Triassic fauna of Symphyta is far from having been studied thoroughly enough for us to insist that Xyelini do, indeed, appear at a later date.

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* The structures located more dorsally than the antennae in the larvae of Siricidae and marked as ocelli (Rasnitsyn, 1969, fig. 261) were identified as such purely tentatively probably ocelli. In any event in Cephidae and Xiphydriidae the ocelli or their rudiments are ~~distinctly~~ located posteriorly of the antennae.

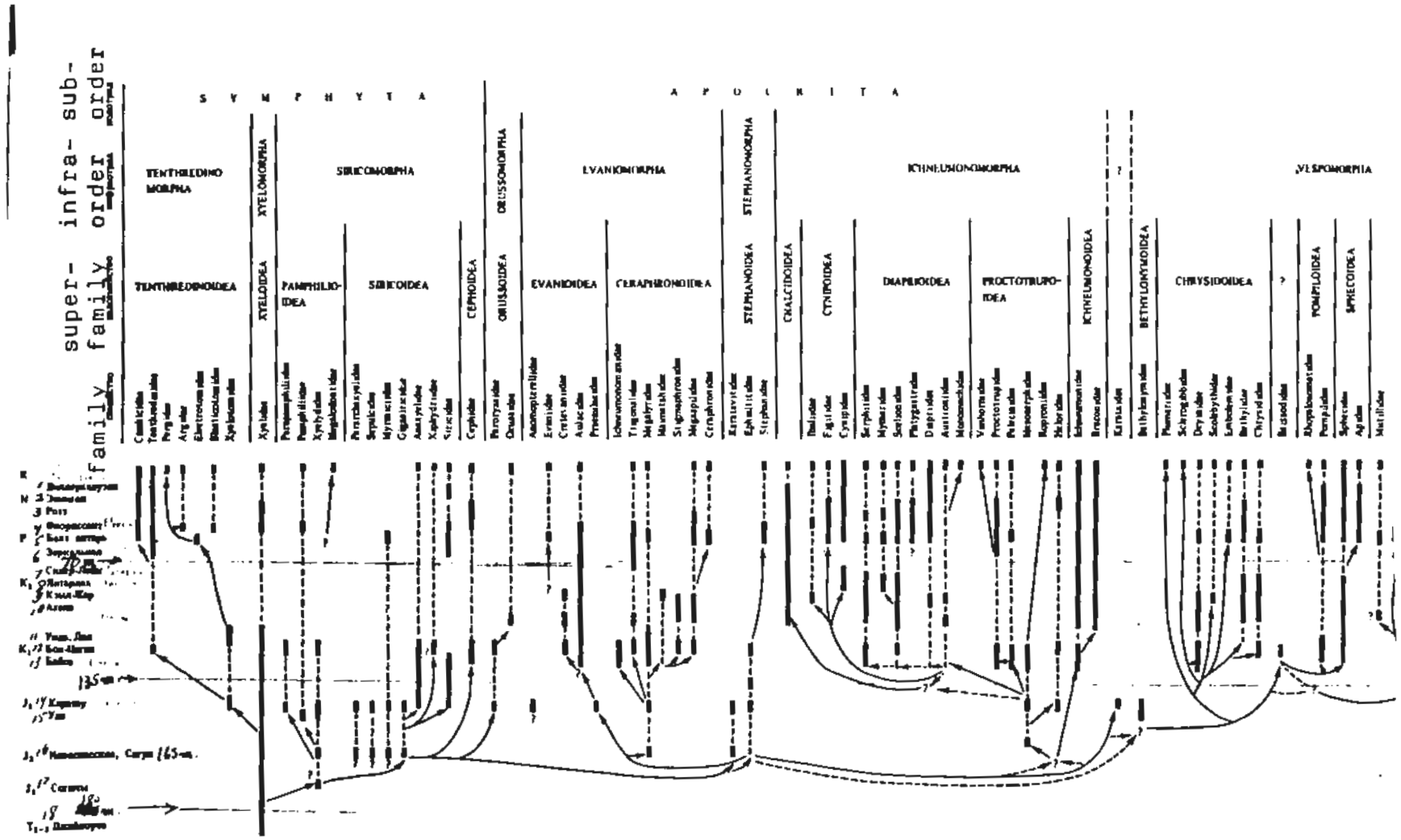


Fig.38. Phylogenetic tree of Hymenoptera

1-Willershausen; 2-Eningen; 3-Rott; 4-Florissant; 5-Baltic amber; 6-Zerkal'naya; 8-Yantardakh; 9-Kzyl-Zhar; 10-Agapa; 11-Unda, Daya; 12-Bon-Tsagan; 13-Baisa; 14-K 16-Novospasskoe, Sagul; 17-Sogyuty; 18-Dzhyailoucho.

Fig. 38

The families of the superfamily Hymenoptera thus break up into three fairly well defined groups: Xyeloidea, Tenthredinoidea and Pamphilioidea+Cephoidea+Siricoidea. We believe that the differences between these groups are significant enough to raise them to the rank of infraorders designated as Xyelomorpha A. Rasnitsyn, infraordo nov., Tenthredinomorpha A. Rasnitsyn, infraordo nov., and Siricomorpha A. Rasnitsyn, infraordo nov., respectively.

Chapter 2

The evolution of Tenthredinomorpha

Tenthredinomorpha are represented by one single superfamily Tenthredinoidea (figs 45-56) and appeared in the geological record in the Late Jurassic age. They may have evolved shortly before that time, since Tenthredinoidea are represented in the Jurassic by a very primitive family Xyelotomidae (figs. 45-46) with a morphology, from which all the other families of that group could be derived. It is interesting to note that Undatoma A.Rasn., the most primitive representative of that family with regard to some of its characters (Rasnitsyn, 1977b), was recorded not from the Jurassic, but from the end of the Early Cretaceous that was marked by a drastic reconstruction of the biocoenoses, as a result of which the ancient (Jurassic or even Permian) relicts sharply increased in abundance and regularly crop up in paleontological collections from that point on. See more details on this subject in Zherikhin (1978).

Tenthredinoidea arose largely as a result of profound modifications in the morphology of the imago (see more detail in Rasnitsyn, 1969). The specialization of their larvae for the open mode of existence which is also associated in the work cited above with the initial stage in the evolution of the superfamily, may have occurred in reality later, in the process of the segregation of two other groups of families (Argidae+Pergida and Tenthredinidae+

Cimbicida) comprising the bulk of the Cenozoic fauna of Tenthredinoidea. This is evident from the structure of the larva of Electrotoma A. Rasn. (fig. 48) found in Baltic amber of the Eocene age (the monotypical family Electrotomidae discussed in greater detail in Rasnitsyn, 1977). The structure of that larva testifies to its existence inside the shoots of some plants or in coniferous cones. Moreover, the endophytic mode of life and many other morphological characters in which Electrotomidae are close to Xyelidae, appear here to have been inherited. p.47

Tenthredinoidea are more advanced than Xyelotomidae and break up into three principal groups: Blasticotomidae, Electrotomidae+Argidae+Pergidae and Tenthredinidae, including Diprionidae+Cimbicidae. The two first groups diverged early, and their primitive representatives (Blasticotomidae and Electromidae) have retained the endophytic mode of life. The third most advanced group comprising the greatest variety of species, arose probably as a group leading an open mode of existence. Blasticotomidae are a product of a relatively early divergence, since their larvae display primitive characters that were lost even in Electrotomidae, such as the median position of the antennaria that are in contact with the frontal margins. The readily observable resemblance of Blasticotomidae to Undatoma from Xyelotomidae was mentioned earlier (see fig. 45). It testifies that Undatoma are close to the ancestors of Blasticotomidae. Electrotomidae were probably ancestral to Argidae and Pergidae, while Tenthredinidae gave rise to Cimbicidae.

As concerns Diprionidae, their rank was lowered to that of a subfamily forming part of Tenthredinidae because of their close links with Tenthredinidae from the subfamilies Nematinae and Susaninae (Smith, 1969). Even the character distinguishing most markedly Diprionidae from Tenthredinidae (i.e. the multitude of their usually pinnate or pectinate antennae) is not particularly radical: the same tendency has been observed in Nematinae of the tribe Cladiini.

The position of the Early Cretaceous larva Vitimilavra paradoxa A. Rasn. (fig. 47) in the system of Tenthredinoidea is not quite clear. With regard to the structure of its head capsule [where the antennaria are in contact with the frons and the eyes are arranged at a considerable distance from the antennaria (in Rasnitsyn's work of 1977 these eyes are erroneously shown as being in contact with the antennaria)] this larva resembles most closely Electrotomidae. However, its shortened antennae and strongly developed limbs, as well as the annulation of its case suggest an open and exophytic mode of existence and constitutes a link between Vitimilarva and larvae of more advanced groups of Tenthredinoidea. The lack of data pertaining to the body structure of this larva makes it impossible for us to definitively determine its phylogenetic position, but the fact that it is close in age to the oldest Tenthredinidae and appeared earlier than Argidae and Pergidae (see farther on) suggests that Vitimilarva may be close to Tenthredinidae.

No Tenthredinoidea other than Xyelotomidae (Upper Jurassic of Southern Kazakhstan) are known from the Jurassic. In addition to the Vitimilarva and Undatoma from the trans-Baykal region that were already discussed earlier, the first, so far undescribed finds of Tenthredinidae were recorded from the Lower Cretaceous of the Mongolian locality Bon-Tsagan. The age of these Tenthredinidae appears to be intermediate between that of Vitimilarva and that of Undatoma (Barremian-Aptian?). The next in time finds belong to the Paleogene, where the other families of Tenthrefinoidea make their appearance.

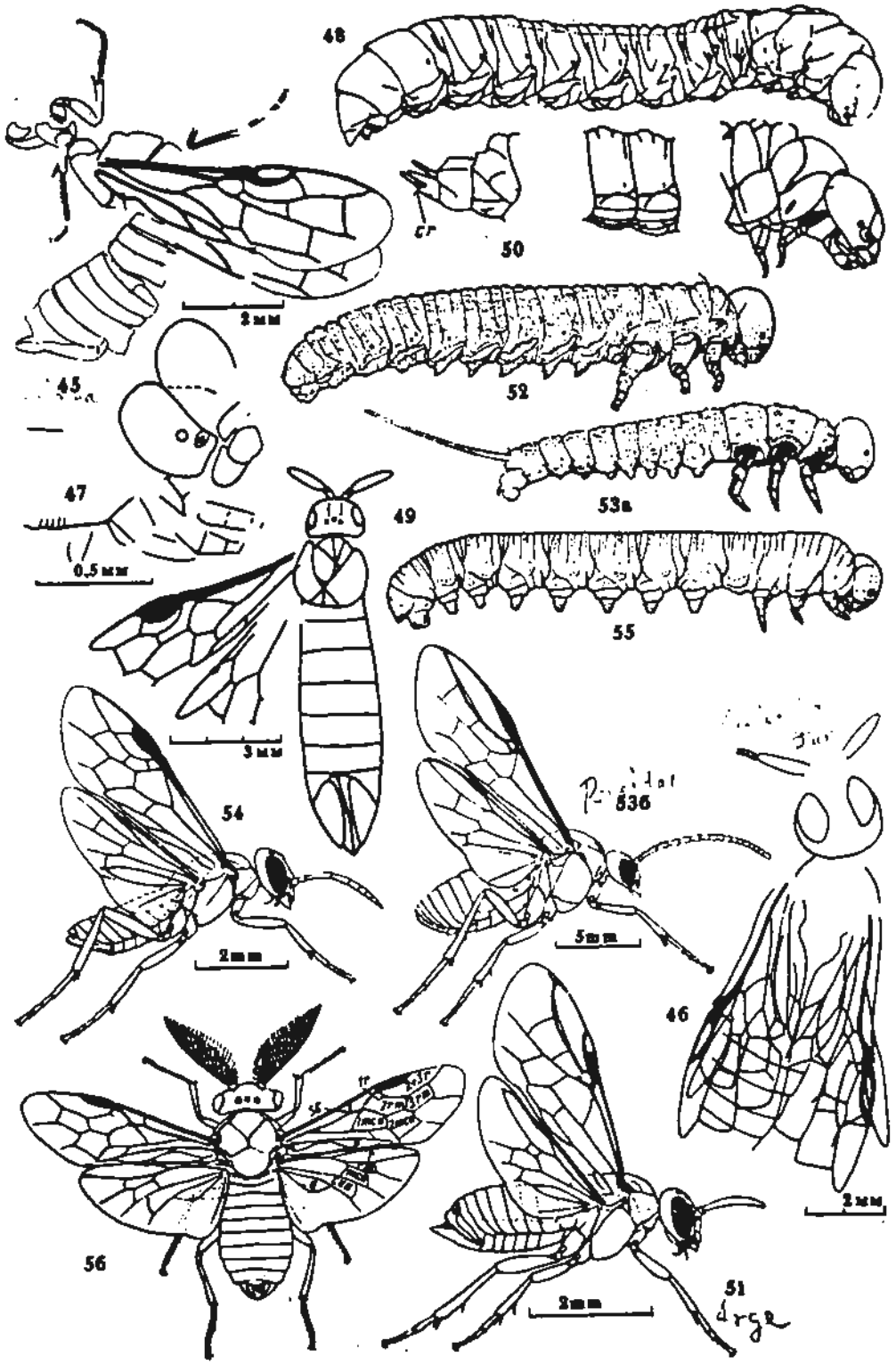
Most of these families are represented in the Paleogene+ Neogene by a mere few finds (no Pergidae have been found in the fossil state, even though their having already existed in the Paleogene age can scarcely be questioned). Tenthredinidae are the only more or less common forms. This family predominates in the living fauna of Symphyta and was equally important throughout the Cenozoic, beginning with the Paleocene (Zerkal'naya river, Sikhote-Alin'). The other families are known from isolated finds in Paleogene deposits and Cimbicidae are also known from the

Neogene*. The Paleocene forms of Tenthredinidae are already quite close to their recent representatives (no genera differing sharply in venation from those living at present have been identified in the fauna from Zerkal'naya, among which primitive Nematinae predominate). These facts suggest that the evolution of the Tenthredinidae fauna of the recent type and the appearance of their living families date back to an earlier period, probably to the middle and latter half of the Cretaceous, when the whole Cenozoic entomofauna arose (Zherikhin, Sukacheva, 1973; Zherikhin, 1978).

Recent groups of Tenthredinoidea poorly conform to Benson's rule (Benson, 1945, 1964) postulating that the primitive Symphyta fed mainly on gymnospermous plants. We are therefore forced to search for their initial hosts among the angiosperms, which appeared for the first time in the Early Cretaceous age and became abundant only in the middle of the Cretaceous (Vakhrameev, 1973); it would appear that the Cenozoic fauna of Tenthredinidae evolved, indeed, in the middle and later half of the Cretaceous period. p.49

* Zherikhin (1978) presents more detailed information on the Cenozoic Hymenoptera.

Figs 45-56


48
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51
drga

Representatives of the superfamily Tenthredinoidea, family Xyelotomidae (45-46) incertae sedis (47) Electrotomidae (48), Blasticotomidae (49-50), Argidae (51-52), Pergidae (53) and Tenthredinidae (54-56).
45-Undatoma dahurica A.Rasn.; Lower Cretaceous, trans-Baykal region; 46-Xyelocerus admirandus A.Rasn.; Upper Jurassic, Southern Kazakhstan; 47-Vitimilarva paradoxa A.Rasn. larva, Lower Cretaceous, trans-Baykal region; 48-Electrotoma succini A.Rasn.; Upper Eocene, Baltic region; 49- Parenphytus ostentus Brues; Upper Oligocene, USA; 50-P. reductus (Malaise), larva; recent; 51-Schizocerella pilicornis (Holmgr.), recent; 52-Arge sp., larva; recent; 53-Philomastix sp., a-larva, b-imago; recent; 54-Caliroa cerasi (L.); recent; 55-Strongylogaster annulosus Norton, larva; recent; 56-Gilpinia polytoma (Hartig); recent (45- from Rasnitsyn, 1977b; 46,47,49 and 50- from Rasnitsyn, 1969; 48- from Rasnitsyn, 1977; 51,53 and 54- from Riek, 1970c; 52 and 55- from Yuasa, 1923; 56- From Bouček, Pădr, 1957).

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In our previous work dealing with the lower Hymenoptera (Rasnitsyn, 1969) we compared the evolutionary paths of these insects / with those of Lepidoptera that are close to them in ecology of their larvae. It was suggested that fertility is in inverse ratio to the individual resistivity, and that ratio was used as a criterion of the morphofunctional progress (Rasnitsyn, 1971a). The use of that criterion allowed us to infer that many Symphyta (least of all Siricoidea) are already much more advanced from the morphofunctional viewpoint than Lepidoptera, i.e. that the evolution of Symphyta along the lines most characteristic of the higher Hymenoptera and, particularly, of Aculeata, was also very intensive. Moreover, in some aspects of the biological progress Tenthredinoidea also did not lag behind Lepidoptera (their abundance determined from the biomass of the larvae in the temperate and particularly, high altitudes; Chernov, Rudenskaya, 1975). However, the relative population dynamics of Symphyta and Lepidoptera has not been studied for the Cenozoic.

It can be done now by comparing the frequency of occurrence of Tenthredinoidea and Macrolepidoptera, the groups most readily comparable with respect to bionomics. Among the other lower Hymenoptera and Lepidoptera there are too many forms that are leading a confined existence, differ from one another in ecological details and are inadequately characterized with regard to their abundance at present. According to the data of V.V. Zherikhin, the percentage of the localities with Tenthredinoidea of the total number of the localities with insects is very stable, at least between the Eocene and Miocene, and comes to about 20%. The only localities taken into account are those with five or more different nonaquatic insects; fossil resins were excluded from the estimates; the data for the Paleocene and Pliocene (50% and 17%, respectively) are unreliable because of the small number of the localities examined. Macrolepidoptera appear for the first time only in the Oligocene, but even there Tenthredinoidea are encountered more often (in 31% of localities); in the Miocene that figure rises to 33%, and in the Pliocene to 55%. Because of the limited number of the Pliocene localities rich in remains, there is no certainty that the increase in the abundance of Lepidoptera during that time is real, but their predominance over Tenthredinoidea in the Pliocene taphocoenoses (though not necessarily in the biocoenoses) is corroborated by the incomparably greater numbers of their remains. The relatively constant frequency of occurrence of the Cenozoic Tenthredinoidea against the background of a sharp increase in the abundance of the higher Lepidoptera (in the Oligocene, perhaps also in the Pliocene) suggests that there may have been little competition between them and Lepidoptera in the course of their evolution. It may be inferred from these data that if the predominance of Tenthredinoidea in the high latitudes and of Lepidoptera in the low latitudes is determined by the competitive interaction of these two groups, then the abundance of Tenthredinoidea is probably the factor acting as an independent variable.

In the recent fauna Tenthredinoidea are distributed very unevenly. Tenthredinidae and Argidae alone are found in all the regions; moreover, the former are most abundant and varied in the Holarctic realm. Cimbicidae and also wide-spread and are lacking only in the Australian realm. Pergidae are most characteristic of the Australian and Neotropical realms, but are also found in small numbers in the Nearctic realm and on Sulawesi island. Blasticotomidae are restricted at present to the Palearctic realm, but during the Oligocene they also existed in the Nearctic realm.

Chapter 3 p.50

The evolution of Siricomorpha

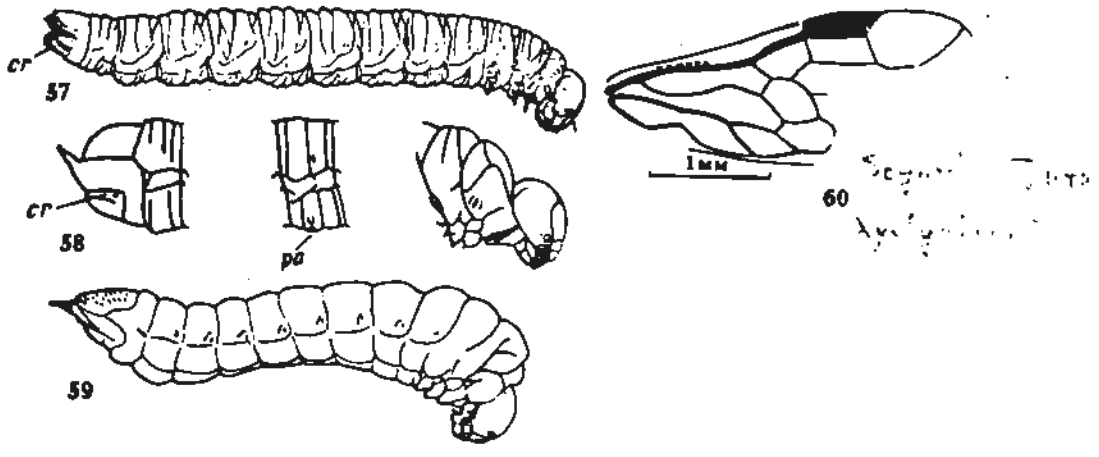
The infraorder Siricomorpha comprises three superfamilies: Pamphilioidea, Cephoidea and Siricoidea (Orussoidea that are commonly regarded as a superfamily close to Siricoidea and are referred to Symphyta, are treated here as part of Apocrita). The evolution of Siricomorpha proceeded essentially along the lines of the optimization of the secretive (confined) existence of their larvae. Even though individual superfamilies differ in the trends of their ecological specialization (Pamphilioidea develop in cobweb nests or, secondarily, inside rolled-up leaves held together with cobwebs, while Cephoidea and Siricoidea develop inside tree trunks, stems, etc.), their morphological modifications display many common features. Without dwelling on the characteristics of the imago that have already been described in detail in an earlier work (Rasnitsyn, 1969), we shall point out only the larval adaptations (figs 57-59). As a result of the confined mode of life the Siricomorpha larvae display no tendency to develop abdominal limbs that are so characteristic of Tenthredinomorpha. The rudiments of pseudolimbs which appeared in Xyelidae, disappear here almost completely (their vestiges may be observed in some Cephidae). On the other hand the subanal appendages (probably homologues of the cerci and limbs of the 11th abdominal segment) undergo a pro-

gressive differentiation, at least at the initial stages in the evolution of that infraorder. The sensory tubercles of Xyelidae located at the top of the subanal lobe of the 10th (in reality 10+11, see Ando, Okada, 1958) abdominal segment, become modified to segmented formations superficially similar to larval antennae, and move forward, towards the corners of the anal opening. These appendages are strongly developed in Pamphilioidea and are found in a more or less reduced state in Cephoidea, but disappear in Siricoidea. It would appear that the completely endophytic mode of life (xylophagy) of the Cephoidea and Siricoidea larvae does not favour the development or at least the retention of segmented subanal appendages, and Cephidae must have inherited them from ancestors with a different ecology. These ancestors could scarcely have been Pamphilioidea or, rather, insects with the type of biology that is characteristic of the living Pamphilioidea, since it is doubtful that their mode of existence could have evolved into xylophagy. It is more probable that the two modes of development arose independently from the existence in more or less mature cones of gymnospermous plants presumed for primitive Xyelidae. It is, however, entirely possible that the larvae of the ancestral Siricomorpha already utilized cobweb even under those conditions (e.g. to seal their shelter against their enemies or some other external factors). We could then readily understand the reasons for the modification of the subanal sensory tubercles into segmented appendages still in the common ancestor of Siricomorpha. Furthermore, it would enable us to explain many other features of resemblance not only by the parallel adaptation under similar conditions, but also by the fact that at least the first stages of the relevant modifications occurred prior to the divergence of the two principal lines of the infraorder. This applies to larval characteristics, such as the more intensive (relative to that in Xyelidae) reduction of the abdominal, as well as thoracic legs, the simplified differentiation of sternites (reduction of the longitudinal and oblique folds), the marked lengthening of the last abdominal segment with reduction of the supporting anal structure (earlier

stages of that process may be seen in Pleroneura, Xyelinae), and the decrease in the size of the head capsule relative to the body diameter, which permits the larvae to penetrate into even narrower crevices. From the morphological viewpoint both the imagos and the larvae of the primitive Siricomorpha resembled probably more closely Pamphilioidea than Cephoidea or Siricoidea. Even though the known representatives of the first of these superfamilies have a number of characteristic specializations (apomorphy), the most important ones among them (the reduction of the ovipositor associated with the transition to a semi-open disposition of the eggs, and the distinctive structure of the head capsule in the imago) have been established with confidence only in the families living at present. The original Pamphilioidea may have been primitive enough to be ancestors of all the other Siricomorpha. It cannot even be ruled out that Sogutia A.Rasm. (fig. 60), the oldest Early Jurassic representative of Pamphilioidea from the Sogyuty locality on the Issyk-Kul' lake, which has been tentatively referred to the family Xyelydidae, belongs in reality to that particular ancestral stock. Even the later (possibly Middle Jurassic) Siricomorpha from the locality Sai Sagul (Fergana), most of which have not even been described as yet, are divided very tentatively between Pamphilioidea and Siricoidea. The scantity of the material makes it impossible to draw more definite conclusions at this time, but future finds may compel us to classify Pamphilioidea as the ancestral stock of Siricoidea.

p.51

Figs. 57-60



Figs. 57-59
Larvae of Siricomorpha (living)
57-Pamphilius sp., Pamphillidae; 58-Syrista parreyssi Spin., Cephidae; 59-Xiphydria sp., Xiphydriidae (57,59- from Yuasa, 1923; 58-from Rasnitsyn, 1969).

Fig. 60
Soqutia leiassica A.Ras., Lower Jurassic, Kirghizia, Xyelydidae? (from Rasnitsyn, 1977b).

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It is thus evident that Siricomorphy arose not later than at the beginning of the Jurassic. Remains of representatives of both principal branches of that infraorder, i.e. Pamphilioidea (species of the family Xyelydidae) and Siricoidea (Gigasiricidae, Sepuicidae, Myrmiciidae and Pararchexyelidae) appear already in deposits of the Early or Middle Jurassic (the locality Sai Sagul in the region of Shuraba, Fergana). No Cephoidea have been found in these deposits, but since they are more primitive than Siricoidea in a number of characteristics (many characters in the structure of their larvae, some details of morphology in the thorax of their imago, and their sectorial saw-like ovipositor instead of the piercing needle-like ovipositor found in Siricoidea), we feel that in the Jurassic times there should have existed, simultaneously with Siricoidea, a separate group ancestral to Cephoidea. We are not discussing Cephoidea as such or, rather, their only family Cephidae, since as far as we know its representatives were associated with angiospermous plants, remains of which (similarly to the remains of Cephidae themselves) appear for the first time in deposits of the Lower Cretaceous (Vakhrameev, 1973). It remains, however, completely unknown whether the Jurassic Siricoidea were endowed with the specializations characteristic of the living representatives of that superfamily. The shape of the ovipositor is usually the only character among those listed above that is observable in the

fossil material, but we ignore, for example, what the ovipositor was like in the most primitive Siricoidea of the family Gigasiricidae (Lower or Middle and Upper Jurassic in Central Asia and Southern Kazakhstan). Among the remains of Gigasiricidae at our disposal only one belongs to a female with its ovipositor intact; moreover, the remain in question is an impression of the insect lying on its back, as a result of which it is impossible to determine the structure of its ovipositor. If future finds disclose that the ovipositor in that group was flat and serriform, we shall be able to regard Gigasiricidae as the most probable ancestors of Cephoidea.

Siricoidea (figs 61-71) attain the greatest diversity and abundance in the Late Jurassic times. Remains of representatives of nearly all the known families of Siricoidea (Gigasiricidae, Anaxyelidae, Sepulcidae, Siricidae and Pararchexyelidae) have been found in deposits of that age from Karatan (Southern Kazakhstan). p.53

Another family, Myrmiciidae*, was found in roughly synchronous deposits of the FRG and Great Britain. The only missing family is Xiphydriidae, remains of which are virtually lacking in the fossil material (the remains tentatively referred to Xiphydriidae, were recently found in new collections from the Barremian-Aptian at Bon-Tsagan in Mongolia). In later deposits Siricoidea decrease sharply in abundance, play a subordinate role, and are found singly among the fossil material. In the Lower Cretaceous there have been found remains of Siricidae, Anaxyelidae and, presumably, Xiphydriidae; in the Cenozoic deposits - of Siricidae and Myrmiciidae; among the living fauna - Siricidae, Xiphydriidae and Anaxyelidae. The first two families are now widely distributed

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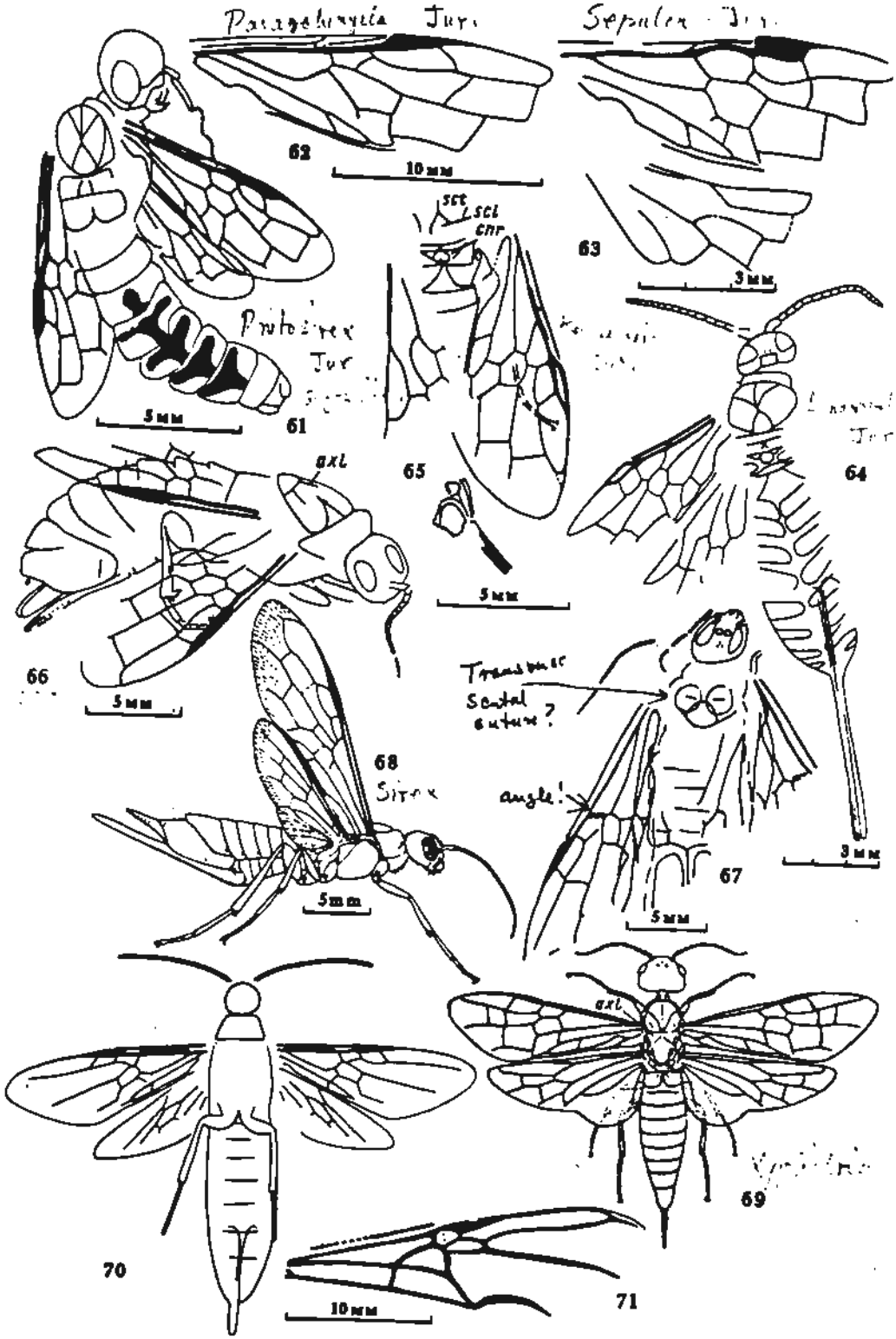
* Myrmiciidae (=Pseudosiricidae) with the size accepted by the author (Rasnitsyn, 1969), is almost certainly a composite group united by features of an intensive reduction of venation. Its representatives have been described mainly from isolated wings and their body structure is poorly known even in the most thoroughly studied Myrmicium (=Pseudosirex) schroeteri (Germar). New finds may compel us to refer many, if not all the genera assigned to Myrmiciidae, to the families that have already been described (first of all to Siricidae), as their aberrant representatives.

(particularly Xiphydriidae that are common in the Southern hemisphere, where Siricidae are practically non-existent) and fairly varied. Anaxyelidae are represented in the living fauna by one single species, i.e. Syntexis libocedrii Rohw. from California.

Figs. 61-71



Representatives of the superfamily Siricoidea. 61-Protosirex xyelopterus A.Ras., Upper Jurassic, Southern Kazakhstan; Gigasiricidae; 62-Pararchexyela macroptera A.Rasn., Upper Jurassic, Southern Kazakhstan; Pararchexyelidae; 63-Sepulca mirabilis A. Rasn.; Upper Jurassic, Southern Kazakhstan; Sepulcidae; 64-Anaxyela gracilis Mart., Upper Jurassic, Southern Kazakhstan; Anaxyelidae; 65-Kempedaja jacutensis A.Rasn.; Lower Cretaceous, Yakutia; Anaxyelidae, Kempendajinae; 66-Aulisca odontura A.Rasn., Upper Jurassic, Southern Kazakhstan; Siricidae Auliscinae; 67-Sinosirex giganteus Hong, Lower Cretaceous, China; Siricidae Sinosiricinae; 68-Sirex noctilio F.; living; Siricidae Siricinae; 69-Xiphydria prolongata (Geoffr.); recent; Xiphydruudae; 70-Myrmicium schroeteri (Germar.), Upper Jurassic, FRG; Myrmiciidae; 71-Eoponera berryi Carp., Eocene, USA; Myrmiciidae (65, 71-original drawings from the holotype; 67-after Hong, 1975, with additional characters from the photograph of the holotype; 68-from Riek, 1970b; 69-from Bouček, Pärd, 1957; all the other illustrations are from Rasnitsyn, 1969).

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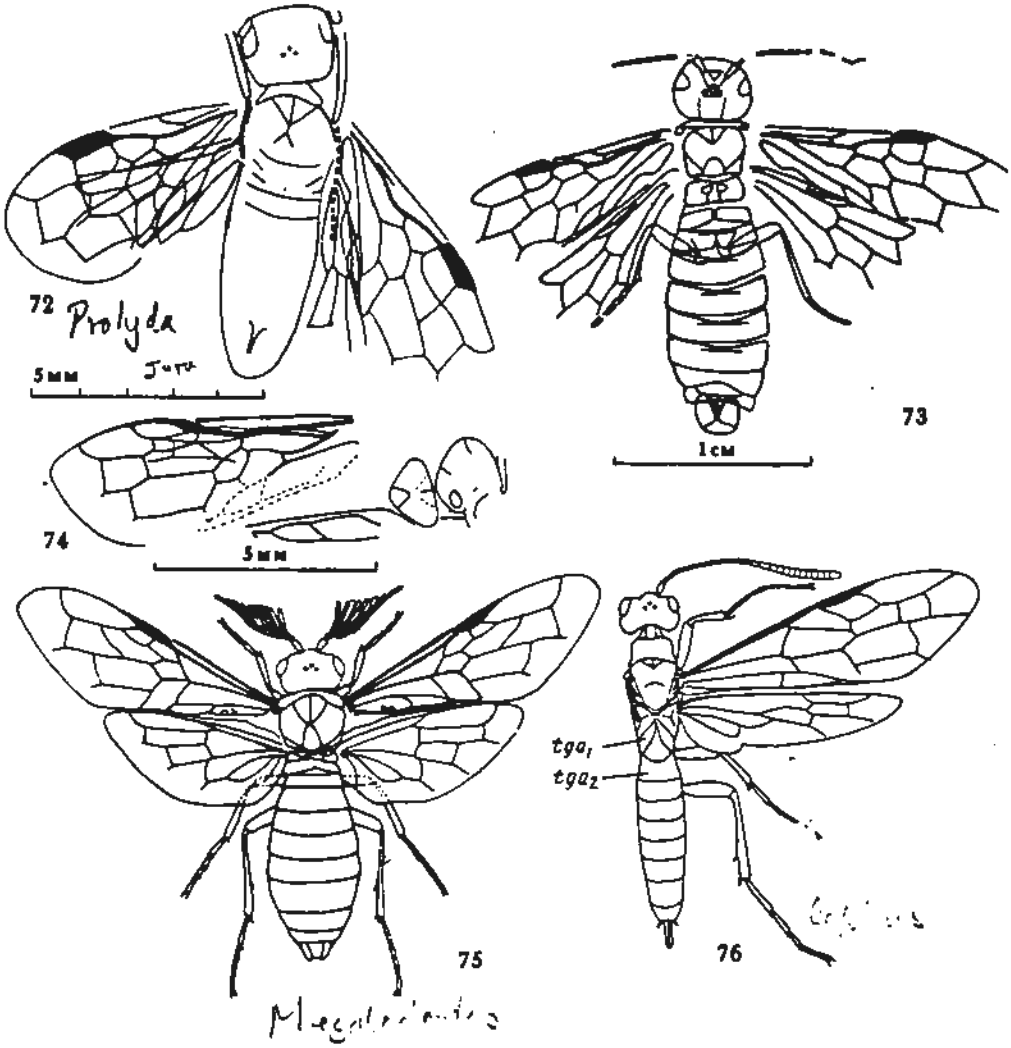
We must add here certain data to those presented in the survey of 1969. First of all it has been proven that Kempendaja jacutensis A.Rasn. (fig. 65), an Early Cretaceous representative of Anaxyelidae, has some very primitive characteristics and merits to be classified as a separate family Kempendajinae A. Rasnitsyn, subfam. nov. with the following diagnosis: scutellum long, with straight lateral edges converging at an acute angle; longitudinal trunk of SC extending far forward beyond SC_1 (as in Pararchexyelidae), developed in the anterior wing; M+CuA of the posterior wing branching more distally than the base of RD, and r-m is located in the distal third of the r cell; the case of the ovipositor sharply downcurved at the base.

Secondly, Eoponera berryi Carpenter, 1929 (fig. 71) from the Eocene deposits in the USA (Puryear in the state of

Tennessee) that was described as an ant, is almost certainly another Eocene representative of Myrmiciidae (their first representative is Megapterites mirabilis Cock. from the Bornemouth in Great Britain, which Euponera closely resembles with regard to the venation of its wing).

Furthermore, the family Sinosiricidae (Hong, 1975) with the only species Sinosirex giganteus Hong (fig. 67) that was recently described from the Early Cretaceous of China, closely resembles Siricidae from the subfamily Siricinae from the viewpoint of venation (except for the distal part of the wing, where the heavy corrugation characteristic of Siricinae, is lacking and the radial cell is closed at the edge of the wing). The body structure of Sinosirex is considerably more primitive than that of Siricinae, but in most of its characters it does not exceed the boundaries of the variability of Siricidae as a whole. The only serious difference is the absence (according to the description) of the transverse mesothoracic suture. If that suture is really lacking, then Sinosiricidae are not only an independent family, but a family distant from Siricidae, their close resemblance in venation and, possibly, head structure notwithstanding (judging from fig. 4 in the work to which we refer the genae of Sinosirex bear deep furrows, in which the bases of the antennae are lodged). This seems to be rather improbable, particularly since a structure that may be interpreted as the transverse suture, can be discerned in the photograph. The inclusion of Sinosiricidae into Siricidae in the rank of a subfamily appears therefore more justifiable than their continued classification as a separate family. p.54

Figs. 72-76



Representatives of Pamphiloidea and Cephoidea
72-Prolyda karatavica A.Rasn., Upper Jurassic, Southern Kazakhstan; Xyelydidae; 73-Acantholyda caplani (Cock.), Upper Oligocene, USA; Pamphiliidae; 74-Parapamphilius confusus A.Rasn., Upper Jurassic, Southern Kazakhstan; Parapamphiliidae; 75-Megalodontes skornjakovi (Freym.), recent; Megalodontindae; 76-Cephus pygmaeus (L.), recent; Cephidae (72-74---from Rasnitsyn, 1969; 75-from Gussakovskii, 1935; 76-from Bouček, Pādr, 1957).

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Phylogenetic relationships of some of the Siricoidea families (Myrmiciidae, Sepulcidae and Pararchexyelidae) are not clear. The other families can be divided into two groups: the primitive families Gigasiricidae and Anaxyelidae (the latter one of which may have descended from the former) and the more advanced families Siricidae and Xiphydriidae, which may have diverged as a common trunk off Gigasiricidae and did so early, probably not later than at the end of the Late Jurassic.

The relationships of the family Pamphilioidea are known even less well than those of Siricoidea. Of the four families belonging to that group (figs 72-75) Xyelydidae and Pamphiliidae are the primitive ones, but each has specializations making it difficult to derive them from one other. Admittedly, the only p.55
apomorphy of Xyelydidae, i.e. the reduction of SC in its hind wing*, has been established only for the Late Jurassic species. Older forms may lack this character, in which case they could be regarded with justification as the possible common ancestor of all the Pamphilioidea. Parapamphiliidae and Megalodontidae are intensively modified, and we have not succeeded in determining their relationship with one another or with the two first families. Xyelydidae and Pamphiliidae have been identified with confidence since the Middle or Late Jurassic (the former family from the Early or Middle Jurassic in Fergana, Late Jurassic in Karatau, Middle and Upper Jurassic localities at Uda in the trans-Baykal region; Pamphiliidae are known only from Uda). Xyelydidae have also been identified (but not described)in the recent collections from the Lower Cretaceous (Barremian - Aptian?) at Bon-Tsagan in Mongolia; Sogutia that was mentioned earlier from the Early Jurassic of Kirghizia (at Sogyuty), may also belong to this family.

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* The second character which was earlier believed (Rasnitsyn, 969) to be apomorphic for Xyelydidae (the absence of the additional transverse cu-** or at least of a bend in M+Cu at its locus, as is the case in Pamphiliidae) could easily be a plesiomorphic feature.

** Illegible. Translator.

Pamphillidae have been recorded not only in the Jurassic, but also in the Eocene (a report concerning Baltic amber that needs to be confirmed), in the Oligocene of the USA (Florissant and Creed ?) and in the Miocene of Primor'e (at Botchi); in the living fauna their range is restricted to the Holarctic regions. Parapamphiliidae have been described from one single poorly preserved remain from the Upper Jurassic of Karatau; the new finds of these forms in the Cretaceous at Bon-Tsagan await description. Megalodontidae are known only from the living fauna of the Paleoarctic regions (there are no fossil remains).

As was mentioned earlier, Cephoidea are represented by one single family, i.e. by Cephidae (fig. 76), and are known from the Lower Cretaceous deposits (from the Neocomian of the trans-Baykal region and from the Barremian-Aptian? in Mongolia). The next /finds of Cephidae/ in time /are rather scant numerically and belong to the Eocene and Oligocene. The living Cephidae comprise two subfamilies, among which Cephinae that are found in the Holarctic regions, are the most diversified and abundant one. All the extinct representatives of the family also belong to Cephidae (SIC). The subfamily Athetocephinae is known from two species of the genus Athetocephus Benson found in Madagascar. Their biology is unknown.

"Konigsmann's (1977) picture of the evolution of the lower Hymenoptera is different from that outlined above. Unfortunately that work appeared too late to be analyzed here in detail. The main differences between "Konigsmann's scheme and ours is his refusal to recognize a) that all the other Hymenoptera descended from Xyelidae, and b) that Siricoidea are related to Cephoidea (in his scheme Symphyta in the narrow interpretation form a sister group of Cephoidea+Karatavitidae+Apocrita). The two propositions (a and b) are interrelated, since it is the denial of the ancestral nature of Xyelidae that enabled "Konigsmann to do the same with regard to Symphyta s.str. and Cephoidea+ Apocrite, even though in doing so he was forced to reduce a large number of similarities between Cephidae and Siricoidea to mere convergences. Since so far the assertion that Xyelidae could not

have been ancestors of the other Hymenoptera, has not been substantiated and the alternative arguments have not been refuted (see the introduction), the two key points of Königsmann's scheme are unacceptable.

PART III

p.56

THE EVOLUTION OF THE HIGHER HYMENOPTERA (SUBORDER APOCRITA)

Chapter 1
The origin of Apocrita

The origin of the higher Hymenoptera, an issue that provoked a lengthy discussion (Handlirsch, 1906-1908; Telenga, 1952; Viktorov, 1959; Malyshev, 1959, 1966; Rasnitsyn, 1968a; Rasnitsyn, 1971), is traced with the help of paleontological material (Rasnitsyn, 1975b). The Jurassic Karatavitidae and Ephialtitidae proved to be the most important groups in this respect (Rasnitsyn, 1963, 1969, 1975a and b, as well as table 3 and fig. 38 in this work). Karatavitidae (figs. 77-78) had been treated until recently as part of Symphyta, since their typical representatives (species of the genus Karatavites A. Rasn.) display no known morphological characters that are substantially different from those of the other lower Hymenoptera, Cephoidea and Siricoidea in particular. Admittedly, Karatavites have a number of features that are characteristic of Apocrita [the reduction of the apparatus holding the folded wings in place, that is composed of cenchri, i.e. coriaceous plates of the metanotum, and a rough field at the base of the anal cellule in the anterior wing; the transverse suture of the mesothorax; a certain constriction of the abdomen between its two first segments (the petiole), i.e. the first step in the formation of the abdominal articulation; the fusion of the two parts of the first abdominal tergite into one single plate; and the needle-shaped ovipositor], which led us at one time to assume that Karatavitidae are close to the roots of Apocrita (Rasnitsyn, 1969). These characteristics have also been encountered in some Symphyta, but never together (one or two per group). In particular the reduction of the cenchri and of the rough field, and the markedly increased mobility of the articulation between the two first abdominal segments are found in Cephidae, while the transverse suture of the mesothorax is characteristic of Xiphyrdriidae and Siricidae.

The needle-shaped ovipositor is developed in all or nearly all the forms of Siricoidea; the undivided first tergite is common among Tenthredinoidea.

The concentration of the features characteristic of the higher Hymenoptera, but encountered occasionally in the lower Hymenoptera as well, does not in itself permit us to refer Karatavitidae to the higher Hymenoptera. But this combination of characteristics is not the only factor to be considered. The many features of similarity between Karatavitidae and Ephialtitidae, a Late Jurassic family with a small number of relicts in the Early Cretaceous (Mongolia, Bon-Tsagan;has not been described), are even more important. There is no longer any doubt that Ephialtitidae belong to the higher Hymenoptera. First of all this is evident from the superficial resemblance of their various representatives (figs 79-82) to parasitic Hymenoptera (mainly to Ichneumonidae, Braconidae and Stephanidae), and, secondly, from the structure of their ovipositor testifying to their parasitic development*. In many Ephialtitidae the ovipositor is very slender and long, sometimes considerably longer than their body. This type of ovipositor functions slowly and requires a great deal of precise and accurate control. Its use is justified only in the cases, where it is necessary to hit a strictly defined point inside a compact and homogeneous substratum, e.g. for laying eggs on a prey living inside wood. As far as we know, the only insects endowed with this kind of ovipositor, in addition to Hymenoptera, are the Permian jugate Archaescitinidae, which probably laid their eggs deeply inside the strobiles of gymnosperms (Bekker-Migdisova, 1972).

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* Here and in the rest of the text we refer to the higher Hymenoptera, after G.A. Viktorov (1976), as parasites rather than as parasitoids, carnivoroids, etc., as is done by many other authors.

TABLE 3

The system of the higher Hymenoptera (suborder Apocrita) adopted in this work

Rank of the taxon	Name	Observations
1	2	3
Suborder	Apocrita	
Infraorder	Orussomorpha	
Superfamily	Orussoides	
Family	Paroryssidae	
Family	Orussidae	
Infraorder	Stephanomorpha	
Superfamily	Stephanoidea	
Family	Karatavitidae	
Family	Ephialtitidae	
Family	Stephanidae	
Infraorder	Evaniomorpha	
Superfamily	Ceraphronoidea	
Family	Megalyridae	
Family	Trigonalidae	
Family	Maimetshidae	
Family	Megaspilidae	
Family	Ceraphronidae	
Family	Stigmaphronidae	
Family	Ichneumonomimidae	Their position within the Evaniomorpha is unclear
Superfamily	Evanioidea	
Family	Praealacidae	
Family	Aulacidae	Including Casteruptiidae Baissidae and Kotujellidae
Family	Cretevaniidae	
Family	Evaniidae	
Family	Anomopterellidae	It has not been proven that they belong to Evanioidea
Infraorder	?	Ichneumonomorpha or Vespomorpha or a group close to their ancestor

Family	Karataidae	
Infraorder	Ichneumonomorpha	
Superfamily	Ichneumonoidea	
Family	Ichneumonidae	Including Pachylommatina (=Hybrizontinae)
Family	Braconinae	Including Aphidiinae
Superfamily	Proctotrupoidea	
Family	Mesoserphidae	
Family	Pelecinidae	Including Pelecinopteridae
Family	Vanhorniidae	
Family	Heloridae	
Family	Roproniidae	
Superfamily	Diaprioidea	
Family	Austroniidae	Including Trupochalcidinae
Family	Monomachidae	
Family	Diapriidae	
Family	Platygastridae	
Family	Scelionidae	
Family	Serphitidae	Including Mymarommatinae
Family	Myramidae	
Superfamily	Cynipoidea	
Family	Ibaliidae	Comprising Liopterinae, Mesocynipinae and Oberthurellinae
Family	Figitidae	Comprising Eucoilinae, Pyctnostigmatinae and Charipinae
Family	Cynipidae	Comprising only Cyniponae
Superfamily	Chalcidoidea	Is not examined in greater detail
Infraorder	Vespomorpha	
Superfamily	Bethylonymoidea	
Family	Bethylonymidae	
	Aculeata	A group of an undetermined rank

Superfamily	Chrysidoidea	=Bethyloidea
Family	Plumariidae	Comprising Heterogyna Nagy
Family	Sclerogibbidae	
Family	Dryinidae	
Family	Scolebythidae	
Family	Embolemidae	
Family	Bethylidae	
Family	Chrysididae	Comprising Cleptidae and Loboscelidiinae
	Aculeata s.str.	A group of an undeterminate rank
Family	Baissodidae	Their systematic positio has not been defined precisely within the interval from the archaic family forming part of Pompiloidea or Sphecoidea, to the separate superfamily at the roots of all the Aculeata s.str.
Superfamily	Pompiloidea	
Family	Rhopalosomatidae	Comprising Harpagocryptu Perk., Olixon Camp., et al.
Family	Pompilidae	Including Ceropalinae
Superfamily	Sphecoidea	
Family	Sphecidae	Comprising Archisphex Evans, Angarosphex A. Rasn., Cretosphex A. Rasn. =Apoidea auctorum
Superfamily	Scolioidea	
Family	Sapygidae	Comprising Fedtschenkiidae
Family	Scoliidae	
Family	Tiphiidae	
Family	Mutillidae	Comprising Myrmosinae and Ticoplinae, Chyphotinae and Apterogyninae
Family	Falsiformicidae	Comprising Taimyrisphex Evans
Family	Sierolomorphidae	

Superfamily	Vespoidea	
Family	Masaridae	
Family	Eumenidae	
Family	Vespidae	
Superfamily	Formicoidea	
Family	Formicidae	Comprising Sphecomyrmina Myrmeciinae, Pseudomyrmicinae and Dolichoderinae
Family	Myrmicidae	Comprising Ponerinae, Cerapachyinae and, tentatively, Dorylinae, Ecitoninae and Leptanillinae

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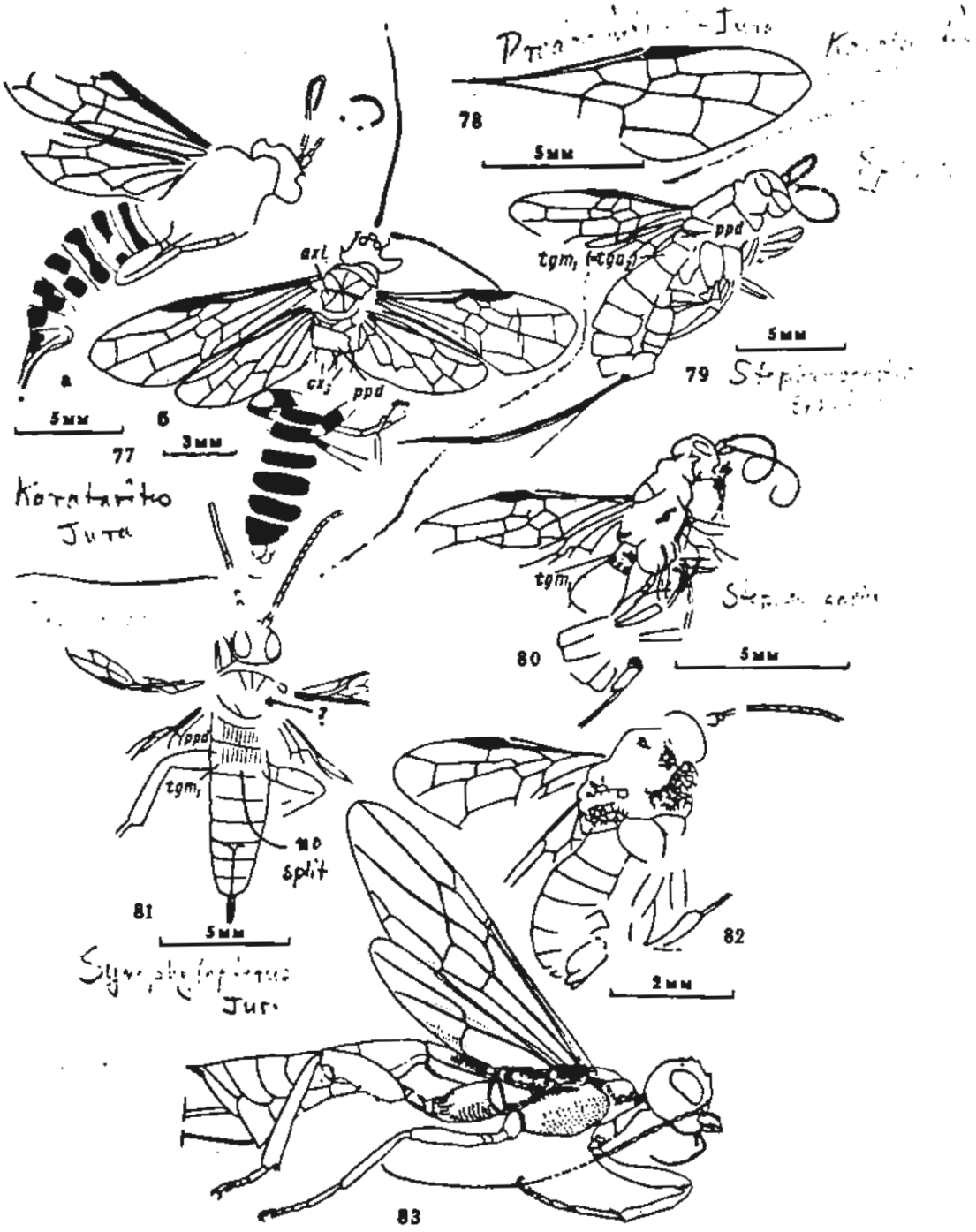
In addition to the complete venation, the feature p.58
distinguishing Ephialtitidae from the other Apocrita is their more or less sessile abdomen. The slender and highly mobile articulation between the first two abdominal segments that is characteristic of the higher Hymenoptera, is still lacking in Ephialtitidae, although they display a distinct /tendency towards its/ formation. The most advanced Ephialtitidae in this respect (see fig. 80) differ but little from the more primitive representatives of Stephanidae (fig. 83), their closest relatives among the living Apocrita, while the others are still so similar to Symphyta that a species of Symphytopterus A.Rasn was even described (from an impression with crumpled wings) as a representative of Siricoidea (see fig. 81). The most primitive forms among those identified beyond doubt as Apocrita on the basis of their most important morphological character are thus virtually indistinguishable from Karatavites, while the biology of the latter (i.e. whether it was a parasite or a xylophage) remains unknown. Karatavites and Ephialtitidae differ in fact only in details of venation of their forewings, and Proapocritus A.Rasn. (see fig. 78) from the Early or Middle Jurassic of Fergana (Sai Sagul) that has been tentatively referred to Karatavitidae, covers that hiatus almost completely (Rasnitsyn, 1975a and b). It is thus evident that Karatavitidae are considerably closer to Ephialtitidae than to any other known group of Hymenoptera and should be united with them not only within the same p.60
suborder, but even within the same superfamily Stephanoidea.

Figs 77-83



Representatives of the superfamily Stephanoidea and of the families Karatavitidae (77-78), Ephialtitidae (79-82) and Stephanidae (83).

77-Karatavites angustus A.Rasn., Upper Jurassic, Southern Kazakhstan; a-female, b-male; 78-Proapocritus praecursor A.Rasn., Lower-Middle Jurassic, Fergana; 79-Stephanogaster magna A.Rasn., Upper Jurassic, Southern Kazakhstan; 80-S. longipalpa A.Rasn., Upper Jurassic, Southern Kazakhstan; 81-Symphytopterus dubius (A.Rasn.), Upper Jurassic, Southern Kazakhstan; 82-Micrephialtites minor A.Rasn., Upper Jurassic, Southern Kazakhstan; 83-Schlettererius cinctipes (Cress.), recent (77a-from Rasnitsyn, 1969; 77b-from Rasnitsyn, 1975b; 83-from Townes, 1949; the other drawings from Rasnitsyn, 1975a).

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Karatavitidae have a more primitive morphology than the other Apocrita and appear in the paleontological record more or less simultaneously with the oldest representatives of the latter (Cleistogaster A.Rasn. from Megalyridae Cleistogastrinae and Paraulacus from Mesoserphidae) during the Early or Middle Jurassic. Karatavitidae were most probably the direct ancestors of all the other Apocrita (or, rather, of all the insects included into that order at present; the meaning of this reservation will be obvious from the further discussion). The problem of the origin of this suborder is thus reduced to identifying the ancestors of Karatavitidae.

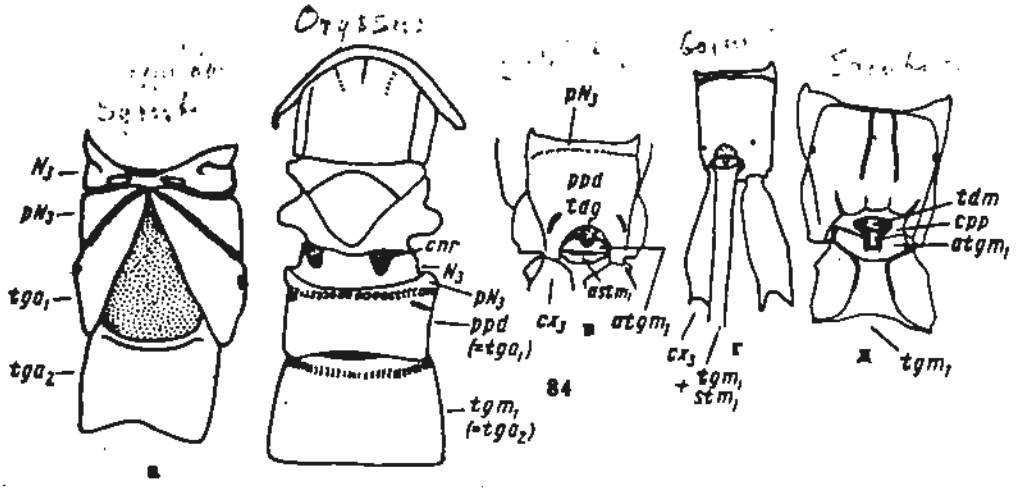
The direct phylogenetic link of Karatavitidae (hence of all the Apocrita) with Siricoidea assumed earlier (Rasnitsyn, 1963, 1968a, 1969) is now questioned (Rasnitsyn, 1975b). Karatavitidae and Ephialtitidae are known only from less than perfectly preserved fossil remains (the impressions found in schists at Karatau and Sai-Sagul reveal considerably fewer structural details than do inclusions in fossil resins or even impressions found in some other, particularly trans-Baykal localities). It is therefore imperative to include into the analysis other representatives of the primitive Apocrita, the living ones in particular, first of all Stephanidae (the closest group to Ephialtitidae). Furthermore, the characteristics of Cephoidea and

Orussoidea must be taken into account. The former were regarded by many authors as forms close to Apocrita (Bischoff, 1927; Ross, 1937; Malyshev, 1959, 1966; Oeser, 1961). Other authors (Rasnitsyn, 1958a) argued, however, against it. Their reservations are based mainly on the characters of the morphological specialization of Cephidae, on their lacking the needle-shaped ovipositor and the transverse mesothoracic suture characteristic of Siricoidea and of the higher Hymenoptera. Orussoidea are similar to Apocrita in parasitic development, which is a highly important characteristic, as well as in some aspects of their morphology (see farther on), but their broadly sessile abdomen and the presence in them of the device holding the folded wings in place make it impossible to regard Orussoidea as a group close to Apocrita (Börner, 1919).

Among the features forming a link between the three groups discussed and contrasting them with Siricoidea we should mention first of all the trend towards a more mobile articulation of the two anterior abdominal segments (fig.84). The mobility of the articulation is a well established fact in Apocrita and Cephidae (in Karatavitidae its mobility is proven by the presence of a constriction between these segments). In Orussoidea the movements of the second segment relative to the first one are less free, but, judging from the position of the furrow on the second tergite, which determines the amplitude of these movements, they are considerably stronger than those between the second and third tergites, let alone those of the articulation between the first tergite and the metathorax. The immobility of the latter is due to the fusion of the posterior division of the metathoracic postnotum (that is downcurved into the body cavity and forms the third phragma) with the anterior margin of the first abdominal segment. Another factor preventing the abdomen from becoming more mobile on account of its articulation with the metathorax is the strongly developed (particularly in Siricoidea, Cephoidea, Orussoidea and Apocrita) second (mesothoracic) phragma. In these forms the phragma occupies a considerable portion of the metathoracic cavity leaving no room for the development of the powerful musculature needed to move the abdomen.

Another character that is similar in the three groups is the structures of the tentorium (the structure of the endoskeleton of the head is unknown for Karatavitidae and other extinct groups). In most of the Symphyta the tentorial bridge is flat and is located on the same level as the base of the anterior pedicels of the tentorium; in Siricoidea, Cephidae, Orussidae and in the higher Hymenoptera the bases of the anterior pedicels are lower than the bridge (fig. 85). Moreover, in Cephidae there appears a median process (corpotendon)* at the anterior edge of the tentorial bridge. This process persists in Orussidae and Apocrita. Lastly, in the two latter groups the bridge grows narrower (very slightly in Orussidae) and, recurving in the form of ⊓ , rises above the other elements of the tentorium. p.61

Fig. 84

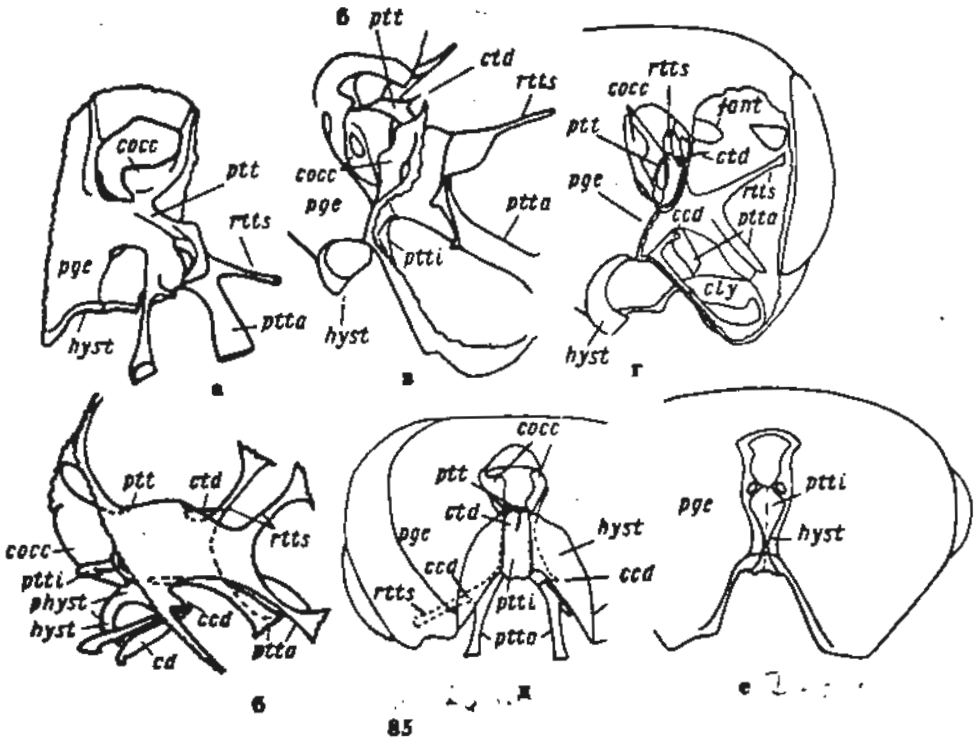


The region of abdominal articulation in Cephidae (a), Orussidae (b), Stephanidae (c and d) and Ichneumonidae (e):

* It is lacking in Syrista knw., but it may be a secondary phenomenon.

a-Syrista parreyssi (Spin.), b-Orussus abietinus Scop, c-Schlettererius cinctipes (Cress.), d-Foenatopus turcomanorum Sem., e-Scambus sp. (all recent, c and e-from Rasnitsyn, 1975b, the others are original drawings).

Fig. 85



Tentorium and posterior wall of the head capsule a-Urocerus gigas L., Siricidae; b-Cephus pigmaeus L, Cephidae; c-Orussus abietinus Scop., Orussidae; d-Rhyssa sp., Ichneumonidae; e-Helcon sp., Braconidae; f-Diplolepsis sp., Cynipidae (a-b---original drawings, c-f---from Rasnitsyn, 1975b).

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A feature characteristic of Siricoidea is the presence of SC in their anterior wing, at least in the form of a cross vein in the costal field (there have been encountered forms lacking this vein, but there is not one single family in which such forms predominate). In the three other groups discussed SC is completely absent. The same groups exhibit the specific tendency towards the reduction of the transverse lr-rs in the anterior wing; moreover,

in all the instances where it has been observed, the reduction begins at the end of the vein adjoining the stigma. p.62

Orussidae are similar to Apocrita from the viewpoint of biology (they parasitize insects, primarily xylophages), as well as in a number of morphological characteristics. As was mentioned earlier, their tentorial bridge is recurved in the form of a ⊓. The head capsule is furnished in both groups (in Apocrita primarily) with postgenae that are closed along the median line between the occipital and oral openings (figs 85 a-d). In most of the Symphyta the head capsule is not closed at that spot or is closed by a secondary plate that may be tentorial in origin, or by closed hypostomes. Only in Siricidae and, judging from the data of Ross (1937), in Anaxyelidae Syntexinae are the hypostomes supplanted by closed postgenae (see more detail in Rasnitsyn, 1969), as is the case in Orussidae and Apocrita. But at least in Ciricidae the crests forming the downward extension of the posterior pedicels of the tentorium, are then abbreviated and do not close (fig. 85a). On the contrary, in Orussidae and Apocrita they follow, as usual, the boundary between the hypostomes and the postgenae and coalesce at the place of the closure of the postgenae forming an odd crest; farther on, towards the articulation condyles of the maxillae, they diverge once again demarcating a triangular platform (figs 85 a-d). There are no signs suggesting that this platform forms on account of the fusion of sclerites (hypostomes), which increases the probability of its being a homologue of the lower (secondary) tentorial bridge.

The first tergite is undivided in Orussidae and forms a butt joint with the postnotum of the metathorax. This is also characteristic of Apocrita, whereas in the Symphyta other than Orussidae the tergite is divided lengthwise (it is not paired only in some Tenthredinoidea) and is connected with the down-folded apex of the postnotum so that there arises a transverse gap between the segments. The segmentation of the mesonotum in Orussidae (fig. 83b) does not differ significantly from the type of segmentation that is common among Apocrita and may be the primary type in that group: in addition to the complement of

sutures usually found in Symphyta, they have the transverse suture that is also found in Siricidae and Xiphydriidae, as well as supplementary (lateral) longitudinal sutures*. The division of the mesonotum in Paroryssidae is not known.

The distinctive structure of the head in Orussidae is very similar to that characteristic of Stephanidae, one of the most primitive groups of the living Apocrita (the crown of spines on the vertex and the unusual shape of the mandibles; figs 83 and 88). This resemblance obviously has not been inherited from a common ancestor, but has been acquired independently and in a parallel fashion. It should, however, be nevertheless taken into account, since parallelisms indicating similar evolutionary tendencies, hence the presence of a common precondition for their realization, also evidence a probable affinity of the groups linked by them. This type of evidence is, of course, less reliable and should be used with great circumspection.

The presence of numerous characters in common in Cephoidea, Orussoidea and Apocrita suggests that they descended from a common stock. Admittedly, the last two groups exhibit features that are also common for Siricoidea, but are lacking in Cephidae, such as the needle-shaped ovipositor, the transverse suture of the mesonotum and the closed (primarily) postgenae; furthermore, the apparatus effecting the fixation of the folded wings is reduced in both Cephidae and Apocrita, but persists in Orussidae, as well as in Siricoidea. If Cephidae, Orussoidea and Apocrita do, indeed, form a monophyletic group, then the needle-shaped ovipositor and the closure of the postgenae should have arisen in Orussoidea+Apocrita independently of Siricoidea. At the same time this means that the reduction of the apparatus holding the wings in place was also an independent development in

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* Many of the authors dealing with the higher Hymenoptera, particularly with Aculeata, refer to these sutures as parapsidal and designate their homologues in the lower Hymenoptera as notaulae.

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Cephoidea and Apocrita. The parallel development of the two latter characteristics is virtually beyond doubt. Indeed, in the contrary event, if we assumed that the closed postgenae are an inherited characteristic, we would be compelled to place Apocrita and Orussoidea right next to Siricidae thus juxtaposing the latter with both Cephidae and Xiphydriidae, which is highly unlikely. If, however, we accept the view that the cenchri and the rough field on the anterior wing were only reduced once, then the higher Hymenoptera will have to be placed next to Cephidae and juxtaposed with Orussoidea, which resemble them much more closely than Cephidae in most characters (see above).

The assumption that the similarity of Orussoidea and Apocrita to Siricoidea on account of the needle-shaped ovipositor is an inherited phenomenon, does not encounter such obvious obstacles, but it significantly increases the number of parallelisms, since all the characters common for the two groups and for Cephidae proved to be just that. Moreover, it should be kept in mind that, as is well known, the transition from a flat to a needle-shaped ovipositor occurred in Symphyta more than once (at least twice in the genus Xyela Dalm., Xyelidae; Rasnitsyn, 1965b). All this makes the hypothesis postulating the phylogenetic unity of Cephoidea, Orussoidea and Apocrita, more plausible. p.63

The three groups discussed resemble markedly Siricoidea and there is no doubt that their common ancestor was at least close to the primitive Siricoidea of the type Gigasiricidae. The distinctive structure of the antennae in Gigasiricidae (see fig. 61), which they inherited from Xyelidae, is no proof to the contrary, since the modification of the heteronomous "xyelidoid" antennae to the homonomous type was a parallel development that occurred in many different ways in the major stems of Symphyta (Rasnitsyn, 1969).

The common ancestor of Cephoidea, Orussoidea and Apocrita probably had the following combination of characters from among those discussed above: a general habit similar to that of primitive Siricoidea, the bridge of the tentorium with a corpotendon,

the segmentation of the mesonotum similar to that of Cephidae (without the transverse or lateral longitudinal sutures), the apparatus for fixing the wings, a more mobile articulation between the first abdominal tergites, and a flat serriform ovipositor. The head capsule may have been closed, simultaneously by two bridges, as in Cephidae (fig. 85b): the outer hypostomal and the lower tentorial bridge hidden underneath the former*. The fusion of the anterior tentorial pedicels in their basal parts that was described earlier for Orussidae and Apocrita, may be a rudiment of the lower tentorial bridge.

The insect endowed with the characters listed above, cannot, of course, be referred either to Orussoidea, or to Apocrita. It also differs markedly from Cephidae, but the latter is the last and the only known family of Cephoidea, although there were probably others. It is difficult to assert a priori that, when it is found, this ancestor cannot be introduced into the superfamily Cephoidea, but it does seem unlikely.

There remains the problem of the position of Orussoidea: should they be left, similarly to Cephoidea, among the lower Hymenoptera, with which they are currently classified, or can they be referred to the higher Hymenoptera? The solution depends on the sequence of divergences: if Cephoidea were the first ones to split off the common stem with Orussoidea and Apocrita diverging later, then the two latter groups can be united. If, however, Orussoidea or Apocrita branched off first, then amalgamation of this type would result in a polyphyletic taxon which, barring an extreme necessity, it is best to avoid.**

From the viewpoint of the concrete distribution of characters the last variant of the sequence of divergences is the least probable one. It presupposes a closer relationship between Orussoidea and Cephidae than that between each of these

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* The two bridges were mistaken in the past for one single bridge (Rasnitsyn, 1969, p.84).

** The author's view on the problem of polyphyletic taxa is outlined in the work by Ponomarenko and Rasnitsyn, 1971.

two groups and Apocrita, seemingly in the absence of features uniting these two groups and contrasting them with Apocrita. There remain the two first variants, one of which (the early segregation of Orussoidea) implies that they changed to parasitism, acquired an acicular (needle-shaped) ovipositor, a structure of the tentorium and posterior wall of the head similar to that of Apocrita, a segmentation of the mesonotum practically identical to that of Apocrita, and the whole (undivided) first tergite of the abdomen butt-joined to the metanotum, independently of Apocrita. The second variant (the earlier divergence of Cephoidea) permits us to treat the similarities listed above as inherited characters, but demands that the modifications which led the two groups to the reduction of the mechanism of wing fixation in repose, be regarded as parallel developments. Even though there are no other known examples of the independent reduction of that apparatus in Hymenoptera, the last variant appears to be p.64 preferable to the others, since it involves considerably fewer parallelisms. Furthermore, it permits us to include Orussoidea into Apocrita thus providing them with sharply defined biological outlines. In further account we shall therefore treat Orussoidea as part of Apocrita and set it apart as the infraorder Orussomorpha A. Rasnitsyn, infraordo nov.

Proceeding from the above considerations, we can formulate the following hypothesis of the origin of the higher Hymenoptera.

The evolutionary stem Cephidae+Apocrita s.l. may have diverged off the primitive Siricoidea similar to Gigasiricidae or directly off the latter (if the ovipositor of Gigasiricidae was serriform). Its divergence was accompanied by certain modifications in the morphology of the imago, which affected the structure of the tentorium, the relationship between the scutellum and the two first abdominal segments, the venation of the wings and the structure of the antennae (see above). The functional significance of the first and last morphological modifications remains obscure, but the other changes appear to be associated to varying degrees with the improvement of flight.

The problem of the larval biology and morphology is more complex. Living Siricoidea inhabit predominantly dead wood free of fungal mycelium and contaminate it themselves with symbiotic fungi. This has been established for Siricidae and Xiphydriidae (Benson, 1950), but appears to be also probable for Anaxyelidae: according to the data of Middlekauff (1964), Syntexis libocedrii Rohw. settle down on the trunks of Libocedrus decurrens Torr. soon after the tree dies from fire, i.e. prior to the natural onset of fungal infections in the wood. It may be assumed that most Jurassic Siricoidea, at least those in which a powerful needle-like ovipositor has been established with confidence (Siricidae, Anaxyelidae, and Myrmiciidae), developed in a similar manner on the trunks of gymnospermous plants, probably Bennettitales and Cycadophyta, or on coniferous plants with a parallel geographic range (similarly to Siricoidea, these plants were abundantly represented in the Indoeuropean paleofloral realm, but were rare in the Siberian realm; see Vakhrameev et al., 1970).

Unlike Siricoidea, the Cephidae develop on living angiospermous plants, primarily in woody branches and shoots. As was seen earlier, some Xyelinae (Pleroneura) develop in a similar fashion in live shoots, but of gymnospermous plants. Similarly to Cephidae, most Xyelidae have a flat serriform ovipositor adapted for the oviposition inside living plant tissues. It is assumed that the ancestors of Cephidae+Apocrita also had a flat ovipositor. All these facts may be viewed as evidence that the primitive Cephidae inherited many of their developmental features from Xyelidae, from which Siricomorpha descended (we are referring to the development in tissues of living, but gymnospermous rather than angiospermous plants, as was the case with the Cephidae).

The larvae of many Cephidae (see fig. 58) appear to be very primitive from the morphological viewpoint and were little reduced for endophytous larvae. It may therefore be inferred that the ancestors of that family (both their close and fairly distant ancestors all the way to the most primitive Siricoidea) had similar larvae and that the morphological evolution

of the larvae was weak in that line.

The hypothetical ancestral group of Apocrita and Cephidae was thus similar in morphology and biology of their larvae to Cephidae (except, of course, for the taxonomy of their food plants, although their development in the living wood of the ancestors of angiosperms cannot be ruled out); the imago was probably similar in habit to the primitive Siricoidea, but differed from them in certain details of morphology (see above). This group probably arose in the Jurassic age and persisted at least until the beginning of the Cretaceous, since an earlier appearance of the Cephidae associated with angiospermous plants is rather improbable. The evolution of the Cephidae was accompanied by the change of their food plants (transition to angiosperms) and considerable modifications in the morphology of adult individuals (Rasnitsyn, 1969). The general aspect of Cephidae also altered, and they became slender insects with narrow wings and a highly mobile laterally compressed abdomen. p.65

The higher Hymenoptera arose as a parasitic group endowed, similarly to the advanced Siricoidea, with an acicular ovipositor and with larvae reduced (juvenilized) even more than those of the latter superfamily. Primitive Apocrita developed for the most part on larvae of xylophagous insects, which may be their primary characteristic. If this was the case, their hosts were probably larvae of Siricoidea. During the Jurassic there were virtually no other insects, not even beetles, the development of which is definitely known to have been associated with compact wood free of fungi (see Ponomarenko, 1977b). There is another possible variant. Karatavites were probably able to parasitize only insects living under the bark, on slender branches or stems, since they had a short ovipositor and relatively small temples (i.e. weakly developed masticatory muscles attached to the temples), which is not characteristic of the Hymenoptera developing inside compact wood. The same features are characteristic of several genera of Ephialtitidae (Symphytopterus A.Ras., fig. 81, Micrephialtites A.Rasn., fig. 82, Symphyogaster A. Rasn., Karataviola A. Rasn. and Trigonalopterus A.Rasn.1 Rasnitsyn, 1975a). This

group of genera is sufficiently homogeneous to be set apart as a separate subfamily Symphytopterinae A. Rasnitsyn, subfam. nov. differing from the nominal subfamily Ephialtitinae A.Rasn. (which includes all the other described genera of Ephialtitidae) in having a short ovipositor and because of the distal position of cu-a in its anterior wing. Symphytopterinae have both plesiomorphous and apomorphous characteristics relative to Ephialtitinae: they have a more primitive position of the transverse cu-a, but the direction of the base of their RS deviates farther from its initial direction than in some members of Ephialtitidae (Stephanogaster A.Rasn., see figs 79-80). It is therefore unclear which one of the two groups is closer to their ancestor in morphology and biology.

In order to elucidate the primary mode of existence of Apocrita we need first of all information on the body structure of Proapocritus or of forms similar to it, as well as finds of more primitive Ephialtitidae than those known to us at present. But the main inference regarding the parasitizing of the larvae of xylophages by the primitive Apocrita can be drawn even now.

The transition of the larvae of Hymenoptera to parasitism was possible only on condition of their cohabitation with their future prey, e.g. by way of predation during accidental encounters with the larvae (Telenga, 1952; Rasnitsyn, 1968a, 1969; Tobias, 1975a). Distinct traces of this type of behaviour persist among Orussidae, whose larvae actively search for victims in their burrows (Powell, Turner, 1975). This implies a parallel and roughly simultaneous change-over of Siricoidea and of the ancestors of Apocrita from living to dead (or dying) wood. Moreover, the difficulty involved in assimilating the new food stimulated the initiation of their symbiosis with the fungi (in Siricoidea) or the change to parasitism (in Apocrita). The change-over to a new habitat by the two groups may have been prompted by the same factor, such as the improvement of protective reactions by the host plant or the extinction (or at least reduction in the abundance) of the host that had no protective reactions. Their competitive expulsion from the living plant

tissues by some other insects is less probable: for reasons remaining somewhat obscure the abundance of the organisms feeding on live parts of plants (except for seeds) rarely attains under natural conditions a sufficiently high level for the trophic competition to arise (Van Valen, 1973).

The change to the development in compact wood induced a number of similar modifications in the higher Hymenoptera and in Siricoidea: their flat ovipositor altered to a needle-shaped ovipositor and their mandibular muscles grew stronger enabling the adult insect to exit from the wood; the latter development manifests itself in hypertrophy of the temples. Some of the means aimed at perfecting the flight mechanism were also analogous in Apocrita and Siricoidea (the appearance of the transverse suture facilitating the flexing of the mesothorax controlled by the horizontal flight muscles). In all the other aspects the trend of their morphological, let alone biological, evolution was different. The most important characteristic of Apocrita next to parasitism may be their persistance in improving the apparatus providing for the mobility of the abdomen.

Chapter 2 p.66

The early evolution of Apocrita

The infraorder Orussomorpha with its two families Paroryssidae (fig. 86) and Orussidae (figs 87-88) is the most markedly segregated group among the higher Hymenoptera. The family Paroryssidae is known from abundant and varied remains from the Upper Jurassic deposits of the Karatau range (Rasnitsyn, 1968b, 1969). Furthermore, an as yet undescribed orussoid that is intermediate between the two families, but appears to be closer to Paroryssidae, was recently discovered in the Early Cretaceous of Mongolia (Bon-Tsagan). Orussidae are markedly modified from the morphological viewpoint (particularly with regard to the structure of their head, ovipositor and limbs; Rasnitsyn, 1969) and appeared not later than the beginning of the Late Cretaceous. They have now a global range, but are found rarely and are represented by a small number of genera and species. This relict group has almost certainly descended directly from Paroryssidae. From the ecological viewpoint Orussidae are parasites of larvae of insects living in wood, and their recent forms develop on Buptestidae and Siricidae (Burke, 1917; Rawlings, 1957). Judging from the small stature and relatively short ovipositor of Jurassic Paroryssidae, most of them parasitized insects that lived underneath the bark of trees or on slender shoots. Orussidae, at least their larger representatives, search for hosts inside tree trunks. The relatively large stature of many living Orussidae (up to 1cm or larger) may be secondary, as is suggested by the miniature size of their probable ancestors (i.e. Paroryssidae), as well as by the drastic reduction of their venation, a feature commonly associated with a decrease in the stature of the insects and persists as a rule after the secondary increase in their measurements (see more detail in Rasnitsyn, 1969).

The bulk of the higher Hymenoptera forms one single integral monophyletic group which may have branched off their

common ancestor with Orussidae before the Middle Jurassic epoch. At the base of that stem we find Karatavitidae with Proapocritus forming the transition to Ephialtitidae, i.e. to the family from which the adaptive radiation of the higher Hymenoptera really began. The divergence of that phylogenetic line and, to a significant degree, its further evolution are characterized essentially by three fairly stable tendencies. One of these tendencies is the improvement of flight with the resulting reorganization of the venation (the distal shift of the base of RS and reduction of A_2) and narrowing of the wings, the hind wing in particular (at the expense of the jugal lobe), which made it possible to dispense with fixation of the wings in repose. Reduction of the wing-fixation apparatus considerably cut down on the time required for the preparation to flight: first of all the movements disengaging the wings from the cenchri could now be eliminated, and, secondly, it became possible to alter their position at rest. In very many Apocrita the wings in repose are not folded flatly on top of one another, but are raised upwards without touching, thus providing for a greater freedom of wing movements during the take-off.

The second tendency characteristic of the evolution of the descendents of Karatavitidae is the increased mobility of their abdomen. This development appears to be related to a significant degree to the third trend of their evolution, i.e. alteration and optimization of the relationship between the parasite and its hosts. However, this relationship is not very clear. As we shall see from the further account, an increased mobility of the abdomen can be achieved by different means. Moreover, neither the direction of the changes, nor the level of the mobility attained is clearly correlated with the distinctive characteristics of the prey or the mode of its infestation. The series of steps taken by Stephanomorpha for the purpose of improving the abdominal articulation does not, for example, appear to have been accompanied by perceptible changes in their manner of infesting the host larvae. At least the large forms of Ephialtitidae infested larvae of the insects living inside wood;

living forms of Stephanidae are doing the same. But Stephanogaster magna A.Rasn. still has, for example, a very broad and relatively immobile abdominal articulation (see fig. 79), while in Foenatopus Smith, one of the most highly specialized genera of Stephanidae, the articulation is already quite narrow and mobile (see fig. 84d). Furthermore, the posterior propodeal opening of Foenatopus is p.67
separated from the posterior coxal fossae, a feature characteristic of considerably later evolutionary stages of Apocrita. These modifications cannot, however, be regarded as truly cardinal. We may in fact be dealing here with a phenomenon that appears to be wide-spread in evolution: a slow advance towards the optimum within the limits of a stable system of interactions. The situation regarding the optimal type of abdominal articulation attained by the infraorders Ichneumonomorpha and Vesopomorpha, is more complex (fig. 84e; see more detail farther on and in Rasnitsyn, 1975b). For Vespomorpha, which changed to infesting more or less mobile type of prey by way of a direct contact in confined situations in crevices in the substratum, the need to increase drastically the mobility of their abdomen is quite obvious. However, the same type of articulation is found in Ichneumonomorpha, many (the most primitive) representatives of which (primitive Ichneumonidae and Braconidae, the most archaic proctotrupoids from the Jurassic family Mesoserphidae) parasitize larvae of xylophagous insects, similarly to Ephialtitidae. It may, of course, be assumed that primitive Ichneumonomorpha also had a short ovipositor and parasitized mobile insects living in the open, and that parasitism of xylobionts is a secondary (though ancient) characteristic of their progeny. This appears, however, to be less probable, since, first of all, Ephialtitidae Symphytopterinae that are characterized by a short ovipositor and associated probably with insects that lived in the open, are not ahead of Ephialtitinae with regard to the mobility of their abdomen; and, secondly, we know of another example where the improvement of the abdominal articulation was realized in a totally different manner (displacement of the articulation opening far upwards on the propodeum; figs 89-99) by another group of

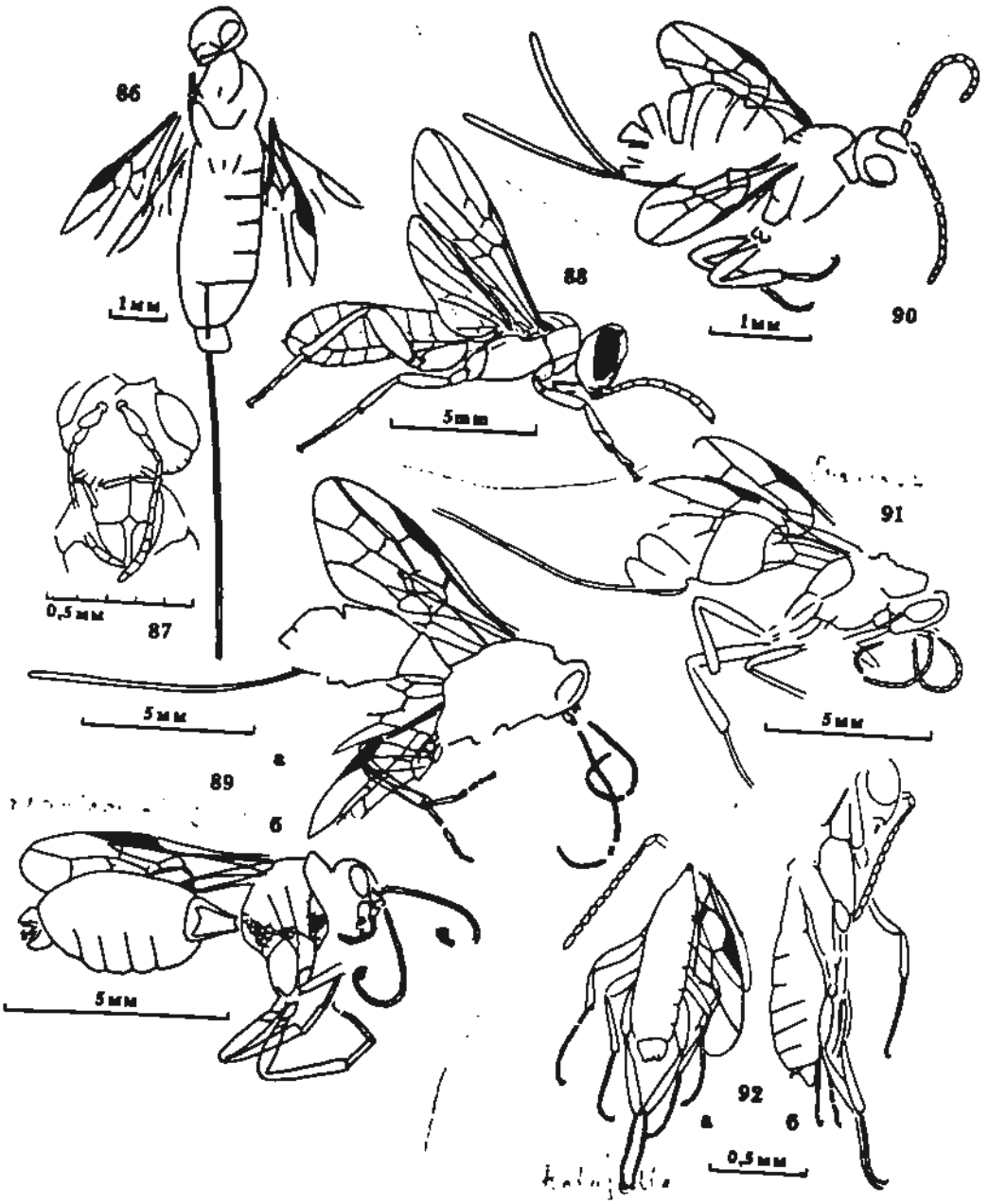
insects parasitizing xylobionts, i.e. by evanoids of the family Praeaulacidae (Rasnitsyn, 1972a). The functional causes of the concrete means employed to increase the mobility of the abdomen are thus far from clear so far.

We should discuss here the problems of terminology arising because the abdominal articulation is located at the boundary of the first and second abdominal segments. Even before it was established that the propodeum is homologous with the first abdominal segment, it became widely accepted in the literature on the higher Hymenoptera to number the abdominal segments beginning with the first postpropodeal segment, i.e. with the segment that is morphologically second, but is regarded as first. The abdomen is actually treated here as a functional rather than a morphological entity. In order to avoid contradictions, there has been proposed (mainly in the foreign literature) the term metasoma that is morphologically neutral and is therefore very convenient for our purpose.

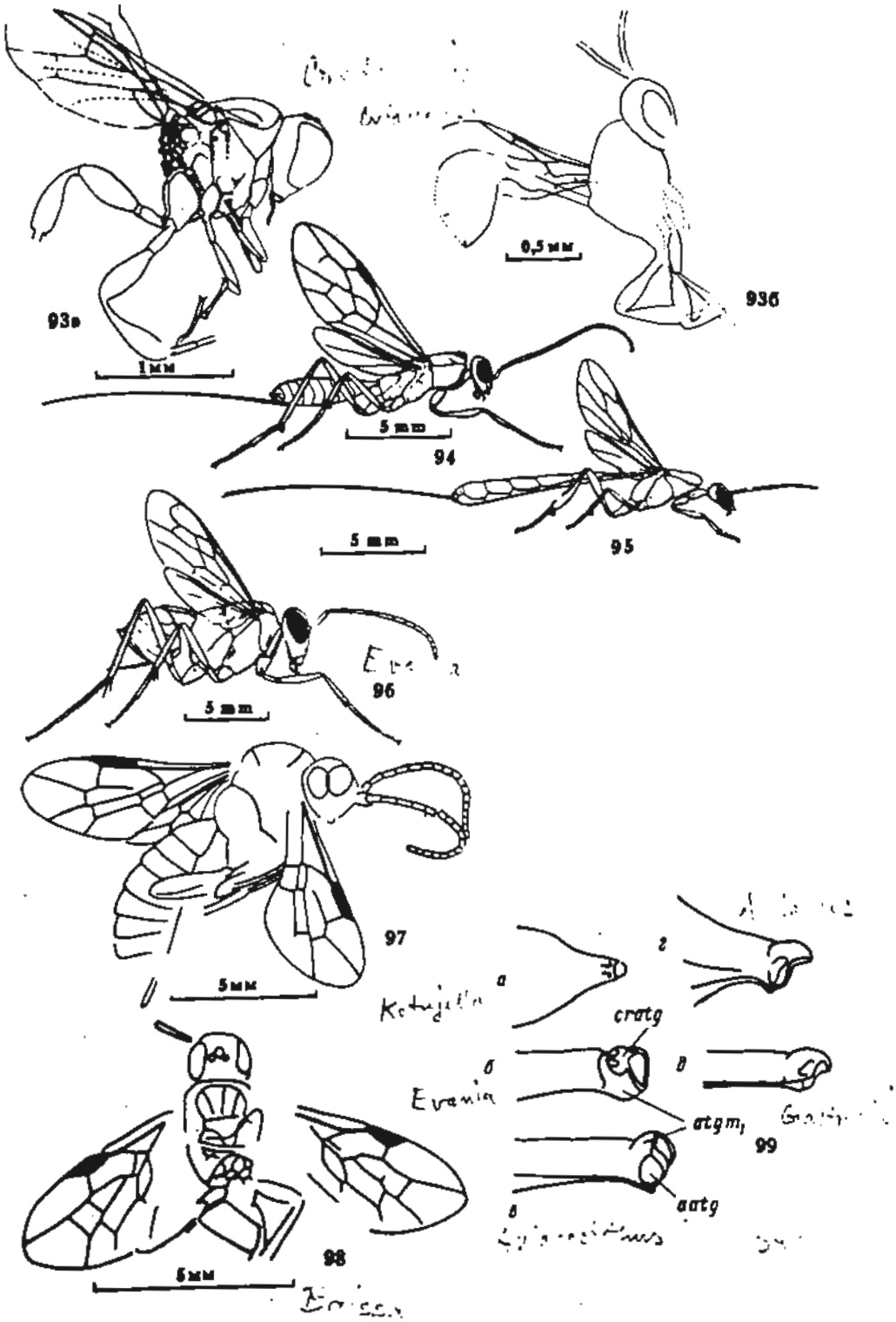
The third major trend in the evolution of the higher Hymenoptera is the alteration of the mode of interaction of the parasite with its victim. This may be the most important factor, since this accounts for the enormous abundance and diversity of the higher Hymenoptera and the crucial role they play in the biocoenoses. It is, however, impossible to analyze this problem in detail. Nor is it really necessary, since there is already a vast literature on the biology and evolution of behaviour of Hymenoptera (Bischoff, 1927; Malyshev, 1962, 1966; Clausen, 1962; Evans, West Eberhard, 1970; Wilson, 1971; Lin, Michener, 1972; Viktorov, 1976; Iwata, 1976). We shall examine only some aspects of this problem pertaining to the processes involved in the segregation of the higher taxa of Apocrita (superfamilies and, in isolated cases, families). We can also discuss here in brief a characteristic aspect of the ecological evolution of the higher Hymenoptera, which, though not universal, is nevertheless widely spread and made a profound impact on the morphology of many groups and on the realization in these groups of the evolutionary tendencies

examined earlier. We are referring to the parasitism of progressively smaller hosts and to the multiple parasitism (i.e. the development of several parasites on the same host) that produces a similar effect. Both these phenomena result in a decrease in the measurements of the insects, which affects, in its turn, the character of their flight and the mobility of their abdomen. The miniaturization leads to the deterioration of the qualities of the insects related to flight, since the conditions of flight become then similar to those characteristic of swimming (Pringle, 1963). The insects respond to it either by refusing p.70 to fly, or by a thorough reconstruction of their flight apparatus.

Figs. 86-92



Figs. 93-99


93a
1мм
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5 mm
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5 mm
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5 mm
96
5мм
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5мм
98
crstg
atgm
99
astg

Figs. 86-88

Representatives of the superfamily Orussoidea
86-Paroryssus extensus Mart., Upper Jurassic, Southern Kazakhstan, Paroryssidae; 87-Mesorussus taimyrensis A.Rasn., Upper Cretaceous, Taimyr, Orussidae Mesorussina; 8-Guiglia sericata (Mocsáry), recent; Orussidae Ophrynopinae (86-from Rasnitsyn, 1969; 87-from Rasnitsyn, 1977b; 88-from Riek, 1970b).

Figs. 89-98

Representatives of the superfamily Evanioidea, families Praeaulacidae (89-91), Cretevaniidae (93), Gasteruptiidae (92,94-95,98), Evaniidae (96) and Anomopterellidae (97).

89-Praeaulacus ramosus A.Rasn., Upper Jurassic, Kazakhstan: a-female, b-male; 90-Praeaulacites minimus A.Rasn., Upper Jurassic, Kazakhstan; 91-Evaniops rostratus A.Rasn., Upper Jurassic, Kazakhstan; 92-Kotujella crucis A.Rasn., Cretaceous (Albian-Cenomanian), Taimyr: a-viewed from above, b-lateral view; 93a-Cretevania minor A.Rasn.; Upper Cretaceous, Taimyr; 93b-Cretevania minuta A.Rasn.; Upper Cretaceous Taimyr; 93b-Cretevania minuta A.Rasn.1 Upper Cretaceous Taimyr; 94-Aulacostethus sp.; recent; 95-Gasteruption sp.; recent; 96-Evania sp., recent; 97-Anomopterella mirabilis A.Rasn.; Upper Jurassic, Kazakhstan; 98-Baissa anomala A.Rasn.; Lower Cretaceous, trans-Baykal region (95-97 from Riek, 1970b; the other drawings from Rasnitsyn, 1975a).

Fig. 99

The base of the metasoma in Evanioidea
a-Kotujella crucis A.Rasn.; b-Evania dimidiata Spin., c-Aulacostethus latreilleanus Nees, d-Aulacus striatus Jur., e-Gasteruption jaculator L. (all of them recent forms; original drawings).

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This comprises the reduction of venation for the purpose of freeing of the veins the outer and posterior parts of the functional wing (i.e. the combined anterior and posterior wings)*, the modification of the shape of the wing, the enlargement, then complete reduction of the pterostigma, and, at later stages of specialization, the development of a fringe on the wings, an increase in the frequency of the wing strokes, often also an increase in the relative volume of the wing musculature, etc. (we already discussed some of these problems in detail; Rasnitsyn, 1969). However, in spite of all these modifications most of the small insects fly more slowly than the large ones, are more vulnerable to attacks by their enemies and less capable of withstanding gusts of wind. p.70

For reasons that are somewhat obscure the miniaturization often leads to a diminished mobility of the metasoma. This is clearly observable in Jurassic Megalyridae of the subfamily Cleistogastrinae (figs 100-101) and among the living forms of Ichneumonomorpha, the smallest representatives of which are sometimes endowed with a secondarily sessile metasoma (many Mymaridae and some Chalcidoidea). Furthermore, small Apocrita often become ephemeral. Imaginal feeding becomes then immaterial, a circumstance reflected in the structure of the mouthparts and associated parts of the head capsule in these insects. In studying the evolution of certain groups, particularly Ichneumonomorpha, these processes must be taken into account.

Oligomerization (reduction of the number of segments) of the antennae is a wide-spread phenomenon associated with the decrease in the stature. It is readily reversible (if the insect increases in size once again, the antennae become polymerized) and may appear to be too trivial to merit a special mention. The existence of the "magic" threshold number of the segments (13-15)

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* According to the data of V.I. Tobias (1977), the outer part of the wing may be also cleared of venation in the event of the adaptation of Hymenoptera to more aride environments. The meaning of this particular factor in the reduction of venation in Hymenoptera needs to be studied further.

that is overcome with difficulty in either direction (during both the oligomerization and the polymerization of the antennae) comes, however, as a surprise. The vast majority of the families and many of the older taxa have either polymerous (commonly with more than 15 segments) or oligomerous (up to 13-15 segments) antennae. The former include Pamphilioidea, Cephoidea, Siricoidea, Stephanoidea and Ichneumonoidea (there are relatively many exceptions among Braconidae, mainly among Aphidiinae and Sclerogibbidae in Vespomorpha). Oligomerous antennae are characteristic of most Xyelidae, Tenthredinoidea (in addition to Diprioninae among Tenthredinidae and to Philomastiginae and Pterygophorinae among Pergidae), Orussidae, Evaniomorpha, Ichneumonomorpha (excepting Ichneumonoidea) and Vespomorpha (excepting Sclerogibbidae). The same applies to the living forms and to other Cenozoic faunae, as well as to the fauna of the Late Cretaceous. During the Jurassic times the division of the families into those with polymerous antennae on the one hand and those with oligomerous antennae on the other, is imperceptible. This suggests that the threshold number of 13 to 15 segments in the antennae arose at the Jurassic-Cretaceous boundary or in the course of the Early Cretaceous epoch.

It is not always obvious that oligomerous antennae are necessarily a consequence of the decrease in the size of the insect occurring in the process of evolution. We have not succeeded, for example, in finding any evidence to that effect for Tenthredinoidea. At first glance this type of causative association appears to be rather improbable for Vespomorpha and Evaniidae, which comprise a significant number of large insects with a complete venation. However, in both cases the ancestral groups (Bethylonymidae and Praeaulacidae, respectively) include small insects with a complete venation and with oligomerous antennae, which may serve as a model of the direct ancestors of the other Evanioidea and Vespomorpha. Furthermore, the Evanioidea which descended from Praeaulacidae, have another character testifying fairly inequivocally to their having undergone miniaturization in the past: the venation of their hind wings

is markedly reduced. The decrease in the overall stature of the insect seems to be almost a prerequisite, but by itself it is not, of course, a sufficient precondition either for the oligomerization of the antennae, or for the reduction of the venation and for the other processes discussed above.

We shall now examine the processes of segregation of the principal evolutionary stems of the higher Hymenoptera (see fig. 38). The numerous descendants of the family Ephialtitidae form five main groups. One of them comprises one single family (Stephanidae) which has currently a large range, but is represented among the living fauna by rare poorly diversified forms. Stephanidae are markedly specialized in a number of characters (in their distinctive general appearance, the structure of their head and limbs, the hind ones in particular, their narrow wings with a markedly reduced venation testifying to their having undergone a significant reduction of the body measurements at some evolutionary stage, etc.). At the same time they display, however, many archaic characteristics, among which the most important one is the primitive structure of their abdominal articulation. From the viewpoint of that character the primitive Stephanidae differ little from some representatives of Ephialtitidae. We have not succeeded in establishing any links between Stephanidae and other Apocrita, and they have therefore been classified as a separate superfamily (Stephanoidea) and infraorder (Stephanomorpha), to which we also refer Karatavitidae (Rasnitsyn, 1975b). Stephanidae may be regarded as descendants of the Ephialtitidae that have been modified least with respect to their taxonomically important characters. This family is known in fossil state only from the Eocene and Oligocene (Zherkhin, 1978). p.71

In spite of the affinity between Stephanidae and Ephialtitidae, the hiatus between them is fairly deep and well-defined. The situation with regard to Megalyridae is totally different. Representatives of the nominal subfamily Megalyrinae (including the Dinapsini) are known since the middle of the Cretaceous. They are characterized by a markedly constricted and fairly mobile, though not specialized abdominal articulation, a

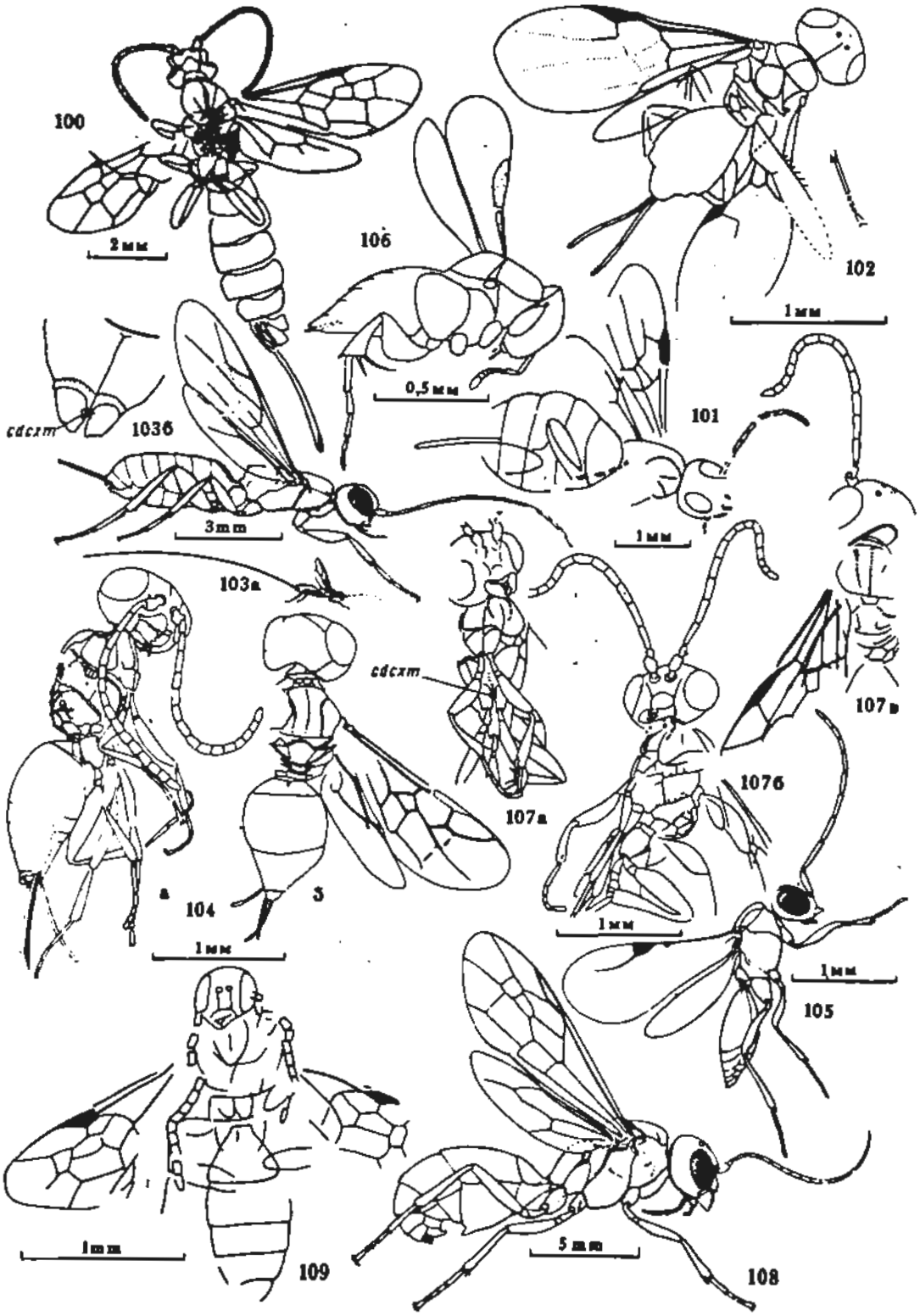
distinctive and markedly reduced venation of the wings, and certain other features (furrows on the head in which the bases of the antennae are lodged, a reduced number of hooklets on the anterior margin of the hind wing, etc.) However, the morphological hiatus between them and Ephialtitidae is almost completely filled by the Mesozoic subfamily Cleistogastrinae (see figs 100 and 101). The smallest and most markedly reduced representatives of that subfamily, such as the species of the genus Microcleistogaster A.Rasn., are particularly close to Megalyrinae, especially to their Late Cretaceous representatives (see figs 101 and 102). On the other hand their primitive forms, particularly those from the genus Cleistogaster A.Rasn., still perceptibly resemble Ephialtitidae. The only diagnostic feature distinguishing the two families is the reduction of the free end of Cu in the hind wing, and it would scarcely merit much attention (in other groups this feature is often used as the criterion for differentiating close genera or even species) if it was the only thing. The divergence of Megalyridae off Ephialtitidae was accompanied by substantial modifications, such as the constriction of the abdominal articulation, but the newly acquired character had not become stabilized in them as yet, and many Cleistogastrinae, particularly their smaller forms (Brachycleistogaster A.Rasn. etc.) often have a secondarily sessile metasoma. The boundary between these two families is therefore much sharper in reality than may be assumed from the diagnosis. But the hiatus as such is not great enough to justify the allocation of the two families to different superfamilies, let alone different infraorders. And yet this is precisely what we are compelled to do, since Megalyridae (in particular Claistogastrinae of the type of Microcleistogaster) are linked by a smooth transition with typical Ceraphronoidea via the family Maimetshidae (fig. 104) (see more detail in Rasnitsyn, 1975a). Ceraphronoidea were included earlier into Proctotrupoidea as the only family Ceraphronidae. Their resemblence to Proctotrupodea is, however, entirely superficial and Masner (1956) set Ceraphronidae apart as a separate superfamily. Later on (Masner, Dessart, 1967) the group was divided into two families

Ceraphronidae and Megaspilidae (fig. 105), to which Kozlov (1975) subsequently added the third family Stigmaphronidae (fig. 106) from the Late Cretaceous. The fact that the transition from Cleistogastrinae to Ceraphronidae was smoother than their transition to Ephialtitidae led us to include Megalyridae into Ceraphronoidea rather than into Stephanoidea (Rasnitsyn, 1975b).

In addition to the families listed above we should also refer to Ceraphronoidea the family Trigonalidae, typical representatives of which (fig. 108) differ fairly markedly from the other Ceraphronoidea, but the hiatus between them and the latter is filled to a significant degree by the Late Cretaceous Cretogonalinae (fig. 107). Trigonalidae have a distinctive biology (Clausen, 1962) in that they lay their minute and numerous eggs on plant foliage. The larva emerges only after the egg has been devoured p.73
by the caterpillar of a moth or by the larva of a sawfly. Some Trigonalidae develop as primary parasites of sawflies, but more commonly they parasitize larvae of Tchneumonidae and parasitic flies. Even more frequently Trigonalidae emerge from the larvae of Hespidae reared on infested prey.

Evanioidea are probably the closest relatives of Ceraphronoidea (see figs 89-99). They have one single apomorphic feature in common: the distinctive joint of the mesacoxae with the mesathoracic postepisterna. The postepisterna then form medially a long process overlapping the coxa and forming the joint on its surface (figs 103b and 107a). In the other Hymenoptera the postepisternum articulates with the edge of the coxa, but in spite of its often being markedly elongated, the resemblance remains purely superficial. For example, in some Specidae the postepisternum overlaps externally the coxa, but the joint is really located at the edge of the coxa, which is deeply notched underneath the postepisternum.

Figs. 100-109


100
2мм
106
0,5мм
102
1мм
cdcxm
103б
3mm
101
1мм
103а
cdcxm
107в
107а
107б
а
104
3
1мм
1мм
105
1mm
109
5мм
108

Figs 100-103
Representatives of the family Megalyridae
100-Cleisterogaster buriatica A.Rasn.; Lower-Middle Jurassic, trans-Baykal region; Cleistogastrinae; 101-Microcleistogaster leptocera A.Rasn.; Upper Jurassic, Kazakhstan; Cleistogastrinae; 102-Cretodinapsis caucasica A.Rasn.; Upper Cretaceous (Lower Cenomanian), trans-Caucasus, Megalyrinae Cretodinapsini; 103a-Megalyra sp., recent; 103b- M. fascipennis Westw.; mesothorax viewed from below (100-101 from Rasnitsyn, 1975a; 102- from Rasnitsyn, 1977b; 103a- from Riek, 1970b; 103b-original drawing).

Figs 104-109
Representatives of the superfamily Ceraphronoidea, families Maimetshidae (104), Megaspilidae (105), Stigmaphronidae (106), Trigonalidae (107-108) and Ichneumonomimidae (109).
104-Maimetsha arctica A.Rasn.; Upper Cretaceous, Taimyr: a-view from above, b-lateral view; 105-Conostigmus sp.; recent; 106-Stigmaphron orphne Kozl., Upper Cretaceous, Taimyr; 107-Cretogonalys taimyrius A.Rasn.; Upper Cretaceous, Taimyr: a-viewed from below, b-lateral view, c-view from above; 108-Taeniogonalos sp.; recent; 109-Ichneumonomima paradoxa A.Rasn., Lower Cretaceous, the trans-Baykal region (104,109-from Rasnitsyn, 1975a; 105, 108 from Riek, 1970b; 106-from Kozlov, 1975; 107-from Rasnitsyn, 1977b).

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The functional significance of the mode of junction of the coxae characteristic of Ceraphronoidea and Evanioidea, is not clear. It is therefore difficult to make any pronouncements regarding its independent development. It nevertheless appears rather improbable that it could have been a vitally important device providing its possessors with significant advantages in their struggle for survival. It is rather a purely external manifestation of some common factors in the organization of the two families (perhaps a characteristic correlated with some other more vital, but so far unknown attributes). But even if this is

wrong, the lack of examples of a reliably established parallel development of this mode of articulation and the infrequent appearance of even superficially similar structures suggest that the probability of parallelisms in this regard is rather low. It is more probable that the similarity between Ceraphronoidea and Evanioidea has been inherited and that we are dealing with a monophyletic group (the infraorder Evaniomorpha; Rasnitsyn, 1975b).

Evanioidea differ from Ceraphronoidea primarily in the trend of development of their abdominal joint. In Ceraphronoidea the articulation opening of the propodeum remains for a fairly long time united with the posterior coxal fossae, and the modification of the first metasomal (second abdominal) segment from an organ assisting in accommodating the contents of the abdomen to a short tube joining the propodeum to the abdomen proper, occurs prior to the closure of the propodeal opening. This point in evolution is exemplified by Maimetshidae, while the next stage, i.e. the separation of the propodeal and coxal openings, is attained only in Ceraphronidae, Megaspilidae, and, possibly, Stigmaphronidae (the structure of their abdominal joint is not known). But even here the base of the metasoma remains close to the coxae.

In Evanioidea the evolution of the ventral joint was entirely different. First of all the abdominal joint narrowed down and closed; thereupon it very rapidly moved upwards and away from the posterior coxae. Even primitive Evanioidea of the kind of the Late Jurassic Praeaulacidae (see figs 89-91) display the position of the abdominal joint typical of that superfamily (Rasnitsyn, 1972a). As was demonstrated by Townes (1950), the upward displacement of the abdominal joint is related to a definite mode of functioning of the long ovipositor, which is squeezed inbetween the posterior coxae to prevent its bending during the boring of wood. p.74

The first metasomal segment may also become modified to an articular tube in Evanioidea (Evaniidae, Cretevaniidae, to

a lesser degree Aulacidae*, see figs 93-96), but, unlike that of Ceraphronoidea, it is not abbreviated, but remains long. Furthermore, a feature characteristic of Evanioidea is a distinctive modification of the head of that segment or, rather, of its acrotergite (see fig. 99). In Praeaulacidae the medial crest, to which the tendons of the muscle raising the metasoma are attached, is short and slender, as in Stephanidae; in Evaniidae it is markedly expanded laterally and backwards, and in Aulacostethus Phil. (Aulacidae) it is even larger, tumid and projects far above the surface of the tergite itself. In Aulacus Jur. and Gasteruptiinae, probably also in Cretevaniidae the crest spreads all over the exterior of the acrotergite and is no longer demarcated as such, while its lateral fossae became displaced to the extreme lateral edges of the acrotergite. The head of the tergite became modified externally to a true spherical articulation head weakly segregated from the part of the segment situated posteriorly, but no spherical joint as such appears to have formed. In any event the abdominal joint of Aulacidae does not appear to be either particularly strong, or capable of rotating the abdomen around its longitudinal axis. It is completely incomprehensible why the final, seemingly readily feasible evolutionary step in the direction chosen by Evanioidea, has not been taken by Aulacidae. Among Gasteruptiinae there are forms with a short ovipositor, where the movements of the metasoma during the oviposition (in bee nests) should be considerably freer than those, for example, of Aulacidae.

Primitive Evanioidea (Praeaulacidae, Aulacinae) parasitize xylophages, Evaniidae develop in the oothecas of cockroaches, and Aulacidae Gasteruptiinae as inquilines in bee nests. The biology of Cretevaniidae is not known.

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* Aulacinae and Gasteruptiinae are regarded here, after Townes (1950), as members of the same family, but the name of the family remains Aulacidae by the right of priority (Aulacidae Schuckard, 1841, versus Gasteruptioninae Ashmead, 1900).

The differentiation of the primitive Evaniomorpha into Evanoidea and Ceraphronoidea appears to have occurred very early, prior to the stabilization of the slender abdominal joint. Indeed, Cleistogastrinae with a not yet stabilized narrow base of their metasoma already exhibit the reduction of venation in the hind wing of the type characteristic of Ceraphronoidea (CuA without the free end, incipient reduction of the ends of RS and M, the straight or, more often, curved outwards segment of M between cu-a and r-m). On the other hand the complete venation with M of the posterior wing curved inwards persists in the primitive Evanioidea (Praeaulacidae), but they already display the upper abdominal joint. Therefore the common ancestor of the two superfamilies must have had, similarly to Ephialtitidae, a primitive venation and a weakly modified abdominal joint. This does not, however, mean that Evaniomorpha are polyphyletic: if, as has been assumed, the characteristic mode of articulation of the mesacoxae evolved in the common ancestor of Evaniomorpha, then this ancestor can be included into Evaniomorpha even if it has a broad abdominal joint.

New finds of Early Cretaceous insects in Mongolian localities make it necessary to amend the systematics of Evaniomorpha outlined in our previous survey (Rasnitsyn, 1975a). This problem will be examined in greater detail elsewhere, and we shall merely present here the most important conclusions. Baissa A.Rasn. from the Early Cretaceous of the trans-Baykal region that was earlier set apart as an independent family, proved to be an aberrant representative of Aulacidae. The same applies to Cretocleistogaster A.Rasn. described from the same deposits among Megalyridae of the subfamily Cleistogastrinae. Kotujellidae found in the resins from the Lower or Upper Cretaceous boundary deposits in Taimyr, also deserves to be assigned to Aulacidae with the rank of a subfamily. The characteristic p.75 features of Aulacidae in this broad interpretation are their external ovipositor, the primitive structure of their abdomen (versus that of Evaniidae and Cretevaniidae), and the numerous signs of their having undergone a general reduction in size: the

reduction of venation, particularly in the hind wing, the commonly semicrescent pterostigma (probably a sign of its earlier increase in relative measurements), and the antennae oligomerized to 13-14 segments.

Ceraphronoidea are supplemented by Ichneumonomimidae (fig. 109) that have been described from the Neocomian of the trans-Baykal region as a possible representative of Ichneumonidea. There is no incontroversial evidence that Ichneumonomima A.Rasn. belong to Ceraphriniodea, but new finds from Bon-Tsagan show that these insects are close to Cleistogastrinae and Trigonalidae.

The paleontological history of Evaniomorpha* begins in the Early or Middle Jurassic, where (the Novospasskoe locality in the trans-Baykal region) Cleistogaster buriatica A.Rasn., the oldest known representative of that infraorder if not of all the higher Hymenoptera, was found. Numerous Megalyridae Cleistogastrinae and Praeaulacidae have been described from the Upper Jurassic deposits of Southern Kazakhstan (Karatau); furthermore, two species of the family Anomopterellidae referred with some reservations to Evanioidea, were also found in these deposits.

In the Neocomian (the first and largest part of the Lower Cretaceous) of the trans-Baykal region there have been recorded only scant remains of Aulacidae (Cretocleistogaster A.Rasn. and Baissa A.Rasn.) and Ichneumonomimidae. In somewhat younger deposits of Mongolia (probably the Upper Neocomian or Aptian; the locality Bon-Tsagan) there have been found the oldest Trigonalidae, one of the last Cleistogastrinae (Leptocleistogaster sp.nov.), Ichneumonomimidae, various Aulacidae (of the type of Cretocleistogaster A.Rasn. and other forms of a more conventional habit) and the first Cretevaniidae, Stigmaphronidae and Megaspilidae that are more common for the Late Cretaceous or (the latter) Cenozoic faunae. In the trans-Baykal region (the

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* Here and in the rest of the text the data on the Mesozoic pertaining to Apocrita are from the works by Rasnitsyn (1975a and 1977b) and those on the Cenozoic are from the work by Zherikhin (1978).

Daya locality; Aptian-Albian?) there has been identified a representative of Cleistogaster dahurica A.Rasn., the most primitive genus of Cleistogastrinae. Aulacidae Kotujellinae have been found in resins from the Albian-Cenomanian boundary deposits in Taimyr, while Cretodinapsis caucasica A.Rasn. belonging to a separate tribe of Megalyrinae, but resembling fairly closely advanced Cleitogastrinae of the type of Microcleistogaster A.Rasn., was recorded in Caucasian resins dated tentatively as Early Cenomanian (Aliev, 1977). In somewhat younger Late Cenomanian resins from Taimyr (Agapa) there have been detected numerous and fairly diverse Stigmaphronidae; Cretevaniidae are there common, though fairly rare; Trigonalidae Cretogonalinae and the last representative of Kotujellinae have also been found in these deposits. Cenomanian Evaniomorpha have not been described as yet, except for Cretevania minuta A.Rasn. and Cretogonalis taimyrius A.Rasn. Stigmaphronidae and Cretevaniidae have also been encountered in later Cretaceous resins: the former in the Turonian-Coniacian (Pachnik, Alaska) and Santonian (Yantardakh, Taimyr) formations, the latter only in the Santonian, where they, as well as Stigmaphronidae, are less numerous than in the Cenomanian. Trigonalidae and Aulacinae are known since the beginning of the Cenozoic (the Paleocene of Primor'e, at Zerkal'naya), Megasilidae and Evaniidae have been recorded in the Eocene. Fossil Gasteruptiinae have been found only in the Burmese amber tentatively dated as Late Cretaceous (Kovalev, 1978).

Orussomorpha, Stephanomorpha and Evaniomorpha constitute the bulk of the infraorders of Apocrita, but comprise only a minor fraction of their families and a negligible percentage of their genera and species. Most Hymenoptera belong to the infraorders Vespomorpha and Ichneumonomorpha. These two groups differ sharply in the trend of their biological and, to a considerable degree, morphological evolution. Vespomorpha comprising the aculeate Hymenoptera (Aculeata) and the extinct Jurassic superfamily Bethylonymoidea with the only family Bethylonymidae (Rasnitsyn, 1975a), diverged off Ephialtitidae as a result of having altered their preying behaviour. While

preserving their association with the insects living inside the substratum (which initially may have been decayed wood), they began to actively search for victims in their shelters and to infest them by way of a direct contact. This led to the appearance of the characteristic "wasp-like" (vespine) body shape, shortening of the ovipositor, and subsequently to its considerable structural modification (in the Aculeata), as well as to the development of an optimal abdominal joint structure, which will be examined in greater detail farther on. The evolutionary course selected by Vespomorpha turned out to be unusually promising. They have succeeded in achieving an enormous biological progress with regard to their abundance, taxonomic and ecological diversity, and in that they act as a major regulator of many biocoenoses (Panfilov, 1961). Furthermore, the organization of Vespomorpha made it possible for them to progressively increase the complexity of their behaviour up to the development of sociality, which raised Aculeata to the highest level of intellectual development among the invertebrates (Mazokhin-Porshnyakov, 1975). p.76

Unlike Vespomorpha, many groups of Ichneumonomorpha have the same biological characteristics as their Ephialtitidae ancestors, i.e. parasitism of the larvae of xylophagous insects. Biological characteristics of the other Ichneumonomorpha have changed, but mainly along the lines characteristic, for example, of Evaniomorpha. Admittedly, there appeared new types of trophic relations, such as the development inside the eggs of insects or inside the seeds, or else the gall formation, but these new trends played a relatively minor role in the biological progress of the group. The main achievements in their struggle for existence comparable to those of Vespomorpha were realized via more traditional trends for which Ichneumonomorpha proved to be better prepared than the other Apocrita.

In particular, among the parasites of xylophages the percentage of Ichneumonomorpha was negligibly small in the Jurassic. In the Upper Jurassic deposits of Karatau there have been found close to 340 identifiable impressions of Apocrita, among

which some 150 impressions belong to parasites of xylophagous insects. Ichneumonomorpha appear to be represented among them by a mere 7-10 specimens belonging to Mesoserphus Kozlov and, possibly, other close genera of the family Mesoserphidae (Proctotrupoidea). So far there are few data on the composition of the parasites during the Cretaceous times, but already at the very beginning of the Cenozoic (the Paleocene in Primor'e, Zerkal'naya locality) Ichneumonomorpha and Ichneumonidae Pimplinae in particular, constitute the overwhelming majority among the parasites of xylophagous insects.

Ichneumonomorpha reign supreme in practically all the ecological niches occupied by the parasitic Hymenoptera in the present-day biocoenoses.

The direction and intensity of the morphological modifications accompanying the formation and further evolution of Ichneumonomorpha differ markedly from those of Vespomorpha. The habit and morphological structure of Vespomorpha are much more uniform than those of Ichneumonomorpha. The evolution of the latter exhibits an unusually strong tendency towards a decrease in the stature, hence the reduction of the venation and of the labiomaxillary complex associated with it, which is not particularly characteristic of Vespomorpha. The main processes of the morphological modifications in the latter (apart from the development of the abdominal joint) appear to have begun fairly late and can be detected in the fossil material only since the Early Cretaceous times. The segregation of the main phylogenetic lines (in particular, the appearance of Proctotrupoidea) and the development of many important morphological modifications begin in Ichneumonomorpha at least during the Late Jurassic epoch if not earlier. The Jurassic Mesoserphidae already display the structure of the head capsule characteristic of that infraorder. We wish to examine it here in greater detail.

As was mentioned earlier, the oral and occipital foramina in the head capsule of the higher Hymenoptera were primarily separated by closed postgenae (see fig. 85). The keels

extending downwards from the posterior pedicels of the tentorium along the inner margin of the postgenae, were fused at the point of junction of the latter forming one single crest, then diverged once again extending towards the condyles that were used for articulation with the cardo of the maxillae. Inbetween the diverging keels there was a triangular plate (the lower tentorial bridge) which was originally (in Orussidae) concealed inside the head cavity, but emerged on the surface already in Stephanidae and is in the middle of the border of the oral opening. This type of structure with various modifications, p.77
including the closing of the genae and formation of the genal bridge instead of the postgenal one (in many Vespomorpha and in Gasteruptiinae among Evaniomorpha), persists in practically all the living Apocrita, except in Ichneumonomorpha. If the labiomaxillary apparatus and, in particular, the cardo of the maxillae becomes elongated, this process is accompanied first of all by the displacement of the maxillary condyles of the head capsule in the laterodistal direction along the edge of the border of the oral opening; the latter reaches the level of the tentorial entries very rarely (only in the higher bees). In Ichneumonomorpha the characteristic elongation of the cardo produces different modifications. The condyles move closer towards one another practically forcing out the outer segment of the lower tentorial bridge, and move forward as a result of the elongation of the posterior part of the border that becomes intergrown with the lower edges of the posterior pedicels of the tentorium (see fig. 85d). At the initial stage of this process, which can be seen only in a few primitive Ichneumonomorpha (Ichneumonidae Pimplinae - Ephialtes Schrank, Rhyssa Grav. and Xorides Latr.), the hypostomal bridge persists. During the subsequent development the elongation of the labiomaxillary complex results in an enlargement of the oral opening to the point, where its posterior edge forces apart the closed postgenae and extends to the level of the posterior tentorial entries; the keels running along the medial margin of the postgenae, diverge somewhat and the lower tentorial bridge fills the maxillary condyles, as well as the interspace thus formed (see fig. 85e). This state is characteristic

of Ichneumonoidea (apart from the genera mentioned earlier and Hybrizon=Pachylomma), Proctotrupoidea (in the size accepted here for that superfamily), most Chalcidoidea, some Cynipoidea, and of Ismarus Hal. among Diaprioidea (see the next chapter regarding the reasons for setting that superfamily apart from Proctotrupodea). In the other Ichneumonomorpha, i.e. in Hybrizon, most Diaprioidea and some of the Chalcidoidea and Cynipoidea, the lower tentorial bridge was secondarily reduced as a result of a decrease in the size of the labiomaxillary complex and/a corresponding shortening of the oral opening. This may have been due to the reduction in their stature and diminished importance of imaginal feeding. The reduction of the lower tentorial bridge occurred independently in different groups of Ichneumonomorpha. Moreover, with rare exceptions, it did not lead to the restoration of the initial situation: as the oral opening grew shorter, the space between it and the occipital opening was filled with the hypostomes rather than with the postgenae (fig. 85f).

Vespomorpha and Ichneumonomorpha therefore followed very different pathways in their biological and morphological evolution. This is particularly surprising, since the two infraorders have an identical and highly distinctive advanced mechanism of the abdominal articulation (see fig. 84e). This mechanism was described by Snodgrass (1933) and later on by Short (1959). The distinctive characteristic of this mechanism is the elongation of the propodeal/condyles/articulation/modified to triangular projections or, more often, to more or less long denticles partitioning off the posterior opening of the propodeum. As a result of this the articulation fossae of the first tergite of the metasoma, which were initially located near its antero-lateral corners, have migrated onto the medial crest of the acrotergite (a formation that may have appeared still in Ephialtitidae and serves for attachment of tendons of the muscles responsible for lifting the metasoma). Deep fossae appeared on the sides of the crest into which the condyles are fitted, so that when viewed in cross-section, the crest is T-shaped.

In some Vespomorpha (Scolia F., Tiphia F.) this development went even farther: the propodean denticles are in contact, and the vertical partition which separated the articulation fossae, disappeared so that the crest changed to a ring strung onto a cross-bar (i.e. the denticles joined together, fig. 194a) and rotating around it together with the metasoma as a whole.

The functional significance of the elongated condyles, i.e. of the displacement of the articulation surfaces towards the median line of the body, is quite clear. The condyles form a transverse axis of rotation controlling the movements of the metasoma in the saggital plane. Furthermore, the articulation provides for a small air gap allowing the metasoma to rotate along the longitudinal axis and to move in the oblique planes deflecting from the saggital plane. The maximum inclination of the rotation plane is determined by the size of the air gap and by the distance between the condyles so that the tangent of the p.78
angle between the rotation plane and the saggital plane is equal in the first approximation to the ratio of twice the size of the air gap to the distance between the condyles. Increase in the mobility of the metasoma and in the maximum angle of inclination of its rotation plane in particular can be achieved either through an increase in the air gap or as a result of the convergence of the condyles. The former way is less promising, since it implies weakening of the joint. The condyles cannot be brought closer together by very much, when it is done by way of a simple narrowing of the articulation opening, since this is the opening through which the internal organs of the thorax and metasoma are connected. Therefore this problem can be solved only in two ways: 1) by replacing the condylar joint with a cup-and-ball type of joint (but it has not been realized even in Aulacidae, which advanced in that direction farther than any other forms), or 2) through the elongation of the condyles and displacement of the articulation surfaces of the second segment onto the bottom of the lateral fossae of its median crest, as was described earlier. The adaptive value of the articulation mechanism characteristic of Ichneumonomorpha and Vespomorpha opens

up the possibilities of interpreting the similarities of these infraorders with regard to that characteristic as a result of the parallel evolution. But to make the hypothesis of the parallelism of Ichneumonomorpha and Vespomorpha convincing, it is imperative to find a causative explanation of their parallel evolution. Since parasitism of xylophages is characteristic of the most primitive Ichneumonomorpha, it may be regarded as an inherited rather than a secondary attribute. Consequently the optimal mechanism of abdominal articulation evolved in these insects under conditions of a relatively stable mode of host infestation. As may be seen from the facts outlined above, under these circumstances other groups modified significantly and improved somewhat their abdominal joint without, however, developing an optimal mechanism. Since it has evolved in Ichneumonomorpha, this group was obviously predisposed to its development, i.e. its makeup facilitated somehow the development of a highly effective abdominal joint.

The mechanism responsible for the development of the ideal joint in Vesomorpha may have been different: it may have been the intensive selection for this characteristic in the process of transition to the method of attacking the prey that is characteristic of this group. However, the transition itself must have been rather difficult for insects with a relatively immobile metasoma. The process which led to the appearance of Vespomorpha can be understood if we assume that they changed to searching for and infesting their prey in confined situations after they acquired a mobile articulation and were therefore pre-adapted to this mode of life. But the group of their ancestors which had a corresponding mechanism of abdominal articulation, but was primitive in all the other respects, may have easily been part of Ichneumonomorpha.

It is difficult to assess the validity of this hypothesis without knowing the concrete characters of the immediate ancestors of Ichneumonomorpha and Vespomorpha. Primitive Vespomorpha (Bethylonymidae) differ from Ephialtitidae only in general appearance and because of their narrow abdominal joint, but we

have not been able to find a group among Ephialtitidae to which they are close. The representatives of Ichneumonomorpha known to us are on the contrary very different from Ephialtitidae and so far no forms transitional between them have been found. The find of Karataidae (fig. 110, Rasnitsyn, 1977b) combining an extremely archaic type of venation with a slender abdominal joint that may be similar to that of Vespomorpha and Ichneumonomorpha, does not solve that problem either: they may have been the ancestors of the two infraorders or a group close to the ancestors of one or both of these infraorders. No characters linking Karataus A.Rasn. to Vespomorpha and Ichneumonomorpha have been detected except for the structure of the abdominal joint.

The relationship between Ichneumonomorpha and Vespomorpha thus remains obscure.

Apart from the structure of the abdominal joint, practically the only synapomorphism of the two infraorders is the presence of "stemming plates" (Hemmplätchen) in most Aculeata and Ichneumonidae and in some Braconidae. The stemming plates (Hemmplätchen) are small membranous lobules on the first valves of the ovipositor serving for evacuating the toxic secretion from the duct of the ovipositor (Oeser, 1961). This author proceeds from the differences in the structure and position of these plates in different groups (in Ichneumonoidea they are usually located in the distal part of the ovipositor and are attached with their capitate base to the fossa on the inner surface of the valve, in the aculeate insects they are borne on the outgrowth of the upper margin of the valve in its basal part, in Betiloidea they are disposed singly on the outgrowth, and in the other Aculeata in pairs) and/the absence of these plates in some representatives of these groups, and he believes the stemming plates to be a character that appeared more than once. The plates of Vespomorpha may, however, easily have evolved from similar structures in Ichneumonoidea, and the stability of their fairly distinctive structure in all the Aculeata s.str. (see below) suggests their secondary reduction (at least in Pompilidae, Sapygidae, Typoctinae, Bradynobaeniday and Vespoidea)

p.79

rather than multiple recurrence. The only factor that does not tally completely with that hypothesis is the presence of the plates in advanced Braconidae (Vipio Latr., Meteorus Hal. and Apanteles Foerst.), and their absence in their more primitive forms (the author analyzed representatives of Helcon Nees, Helconidea Vier. and Doryctes Hal.). It would appear that the presence of the stemming plates in most Vespomorpha and in many of the lower Ichneumonomorpha can nevertheless be regarded as an additional argument in favour of the possible phylogenetic unity of these infraorders.

Chapter 3

The evolution of Ichneumonomorpha

Ichneumonoidea

The superfamily Ichneumonoidea is the most primitive group among Ichneumonomorpha. The morphology of many Ichneumonidae (figs. 111-113) exhibits only minor changes related to the decrease in stature. In particular the reduction of venation in the distal part of the wing manifests itself only in the weakening of the longitudinal veins and in the displacement of the cross-vein 3r-m towards the base of the wing which seems to have been the reason for the disappearance of 2r-m and for the union of 2r and 3r with formation of a characteristic areolet. Moreover, the Early Cretaceous Ichneumonidae (Tanychora Townes) and, to a lesser degree, Tanychorella A.Rasn (Townes, 1973; Rasnitsyn, 1975a) have no true areolet as yet.

Another feature of venation that is common for Ichneumonomorpha, but is not specific of them, and which may have been a result of the decrease in their stature, is the straightening out of the segment of M between the bifurcation M+Cu and r-m in the hind wing. This segment is sharply bent inside the cellule rm in many Ephialtitidae, particularly more primitive ones, in Praeaulacinae (mainly in their large forms) and in most Vespomorpha. There is a certain, but not very strict, correlation between the straightening out of this segment (or even its bending in the opposite direction, as is the case in Megalyridae and Trigonalidae) on the one hand and the decrease in size of the insects on the other. If this assumption is correct, then the large body measurements of Trigonalidae and Evanioidea (excepting the most primitive Praeaulacidae) should be regarded as a secondary characteristic.

In addition to the profuse venation, the primitive characters of Ichneumonoidea distinguishing them from the other Ichneumonomorpha, are first of all the persistance of the postgenal bridge in some of their representatives and the nearly complete absence of individuals with the secondary hypostomal bridge, and,

secondly, the almost always multi-segmented antennae (over 15 segments). These factors are also characteristic mainly of larger insects.

The only factors that may be regarded as advanced (apomorphous) features of Ichneumonoidea making it impossible to derive the other superfamilies of the infraorder directly from this group, are their narrow costal field (closely spaced C and R) and probably the lack of the postspiracular mesothoracic sclerite.

We divide here Ichneumonoidea into Ichneumonidae and Braconidae (figs 111-114). Many authors treat Aphidiidae, p.80
Pachylommatidae (=Hybrizontidae) and, sometimes, Agriotypidae as independent families; moreover, the first two are regarded as groups close to Braconidae, and the last one to Ichneumonidae. Compared to the standard size of families in other groups of Hymenoptera with those of Ichneumonoidea, both Ichneumonidae and Braconidae do, indeed, appear to be too large. These families have a considerably greater diversity and are considerably larger than most of the other families, and it would be rational to subdivide then. However, the division should be done in such a way that the resultant families be comparable with one another. Institution of the three above families achieves little in that p.81
respect, since Ichneumonidae and Braconidae remain nevertheless enormously large and highly diversified groups that are not comparable in size or diversity with the families established and are not separated from them by a sufficiently large hiatus (especially Aphidiidae that are linked to them morphologically, to Euphorinae in particular, by a virtually continuous transition; see, for example, Sarek, 1965, 1969; Tremblay, 1967).

Figs. 110-114

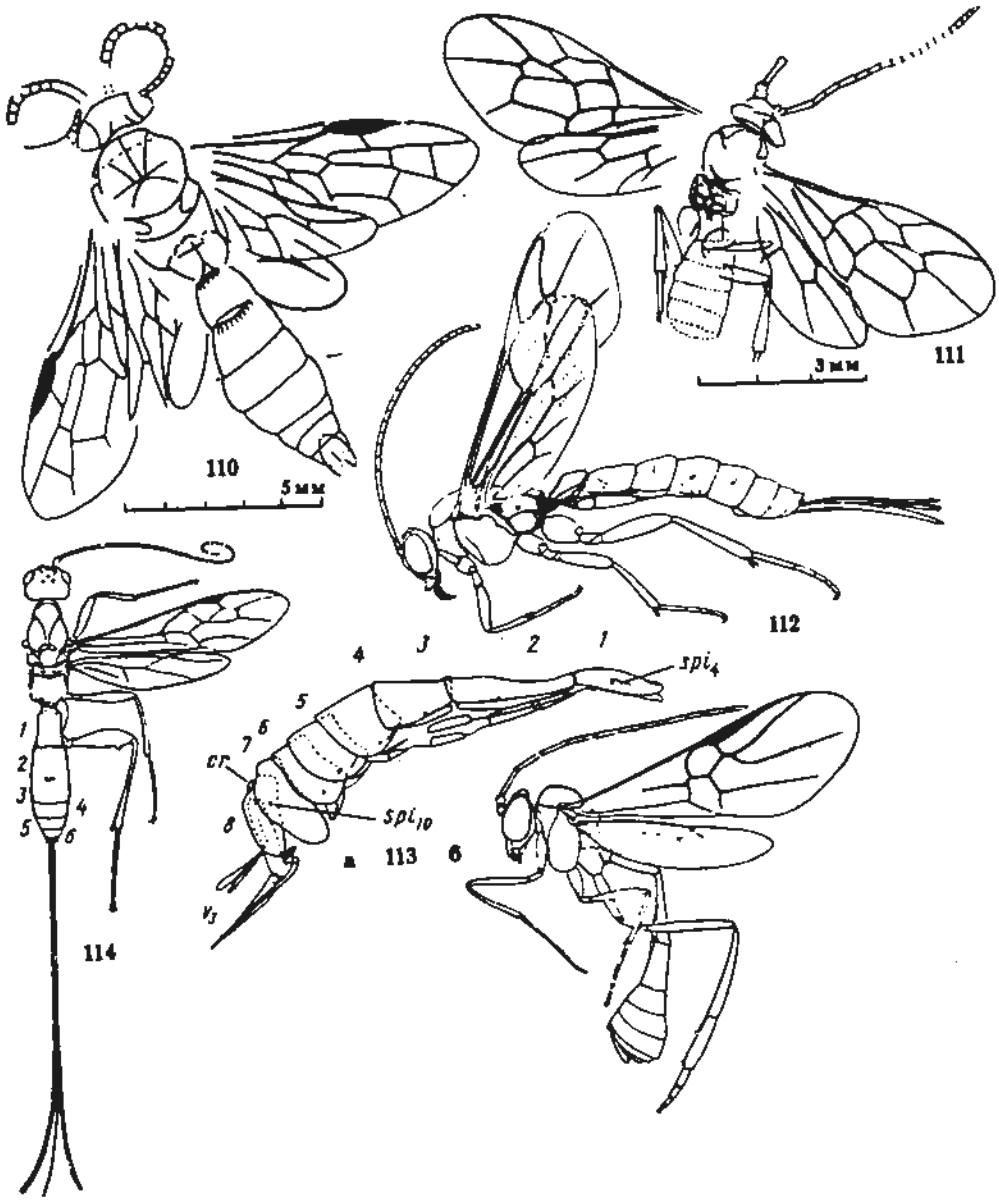

Fig. 110
Karataus pedalis A.Rasn. (Karataidae) (from Rasnitsyn, 1975b)

Figs 111-114
Representatives of the superfamily Ichneumonoidea, families Ichneumonidae (111-113) and Braconidae (114).

111-Tanychora petiolata Townes; Lower Cretaceous, trans-Baykal region, 112-Iserpus stercorator (F); recent; 113-Hybrizon buccatum Breb,; recent; 1-general view; b-lateral view of the abdomen; 114-Helcon sp.; (111-from Townes, 1973; 112-from Townes, 1960, 113a, 114 from Bouček, Stary, 1957, 112b-original).

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However, a more radical differentiation of Ichneumonidae and Braconidae is impossible at the present state of our knowledge; these two families, Ichneumonidae in particular, do not lend themselves to differentiation at this time.

Parallel to this we can examine the systematic position of Hybrizon Fall. (=Paxylomma Brēb.=Pachylomma Först.). As was mentioned earlier, Pachylommatinae (fig. 113) are commonly set apart as a separate family that is believed to be close to Braconidae (Tobiad, 1968), or is treated as a subfamily of Braconidae (Achterberg, 1976a, b). However, the second observable segment of the metasoma in Hybrizon is, indeed, the second segment articulated with the third segment rather than a combination of the second and third segments fused together. Were it not the case, it could not be followed by six tergites bearing spiracles (fig. 113b), since the last (tenth) pair of spiracles is located in insects on the eights (seventh metasomal, respectively) segment. There are therefore no grounds to regard Hybrizon as a form close to Braconidae. The distinctive venation of the wings in Hybrizon is similar to that of Neorhacodes Hedicke and, particularly, in Rhacodopteron Capek. The latter are regarded as aberrant representatives of Ichneumonidae belonging without any doubt to that family; we should probably also refer to it Pachylommatinae.

The similarity of Braconidae and Ichneumonidae is obvious enough. The diagnostics of these families may be complicated and it is rather difficult to formulate their diagnosis in a clear-cut manner, but the boundary between them is nevertheless quite clearly defined (there are no transitional forms; there are only forms secondarily similar in isolated characters; Tobias, 1968). The main differences pertain to the venation of the wings and structure of the metasoma. In Ichneumonidae the venation is normally complete including in particular 2m-cu of the anterior wing (in the smallest forms it may disappear leaving a mere trace, in rare cases it may even disappear completely), the structure of the posterior wing is primitive for Ichneumonomorpha, rm always issues into RS and almost always runs at a considerable distance from its base. In the anterior wing of the Late Cretaceous

and Cenozoic Ichneumonidae, as well as in some of their Early Cretaceous forms (from the Barremian-Aptian of Mongolia, Bon-Tsagan) the cellules 1+2r and 1mcu are fused forming a peculiarly shaped central cellule, and the cellules 2rm and 3rm also coalesce and are modified to a small "areolet". In the Early Cretaceous Tanychora Townes (fig. 111), Tanychorella A.Rasn and in the Ichneumonidae that are close to them, from the trans-Baykal region and Mongolia, these modifications are in an incipient stage: RS+° separating the cellules 1+2r and 1mcu, is complete, though weak; 2+3rm is relatively long, particularly in Tanychora, where it is markedly stretched basally. The systematic position of these primitive Ichneumonidae has not been determined in the original descriptions (Townes, 1973; Rasnitsyn, 1975a), since the characters used as criteria for establishing subfamilies of Ichneumonidae, are unknown for these forms. However, their pattern of venation (particularly in Tanychora) differs fairly markedly from that characteristic of later representatives of the family, enough to justify the classification of at least that genus as a separate subfamily Tanychorinae A.Rasnitsyn, subfam. nov. The systematic position of Tanychorella remains so far rather indefinite.

In the forewing of Braconidae (fig. 11) 2m-cu is always lacking, the 1+2r and 1mcu cellules are commonly divided and 2+3rm is often long. In the posterior wing r-m joins R more proximally than the base of RS, very rarely at the very origin of RS. The second and third tergites of the metasoma are intergrown or even fused in Braconidae without a clearly defined boundary-line between them (in Ichneumonidae they are freely mobile, excepting those of Agriotypus Curtis and Rhacodopteron Capek).

The functional significance of the intergrown second and third tergites of the metasoma in Braconidae and of the formation of the central cellule and areolet in Ichneumonidae is unclear. The other characters in which the two families differ, are related to their size and evidence that the formation of Braconidae involved their progressive miniaturization. Braconidae are even p.82

now smaller on an average than Ichneumonidae and their advanced groups are commonly smaller than the primitive ones (Tobias, 1975b). This, however, does not necessarily mean that the large measurements of primitive Braconidae are primary. It appears more probable that the primitive characters of these forms persisted on account of their early secondary increase in size. The argument advanced by Tobias (l.c.) in support of the opposite viewpoint may turn out to be evidence testifying in favour of our hypothesis. We are referring to the larger stature of many tropical Braconidae. It would appear that the tropical biota is not older than the others, as is commonly believed, but, on the contrary, is much younger, at least relative to the subtropical and temperate biotas (Razumovskii, 1971; Zherikhin, 1978). Admittedly, this applies to the tropics in a narrow sense (Razumovskii, 1.c.). It is therefore imperative to determine more precisely whether the largest Braconidae come from the tropical or subtropical regions. But even if large Braconidae concentrate in the subtropical regions, it cannot be accepted without reservations as proof that the large size is a primary character, since it is too improbable that reduced venation of the kind observed in Braconidae can be found in insects measuring over 5-7mm. Tobias himself notes in his later work (1977) the correlation between the reduction in venation and the decrease in the size of Braconidae.

From the phylogenetic viewpoint Braconidae are probably descendants of primitive Ichneumonidae of the type Tanychorinae, which display no significant autapomorphisms relative to Braconidae, excepting a somewhat weaker RS+M. The late (in the middle of the Cretaceous period) appearance of Braconidae in the paleontological record (Albian-Cenomanian resins from Taimyr), later than that of Ichneumonidae, which make their appearance at the beginning of the Cretaceous (the Neocomian of the trans-Baykal region), also testifies in favour of this hypothesis. However, Braconidae acquired their recent generic composition very early: all the Late Cretaceous Braconidae identified thus far (Santonian and Campanian, no forms older than that have been identified as yet) belong to recent genera. Among the Cretaceous Ichneumonidae there

have been identified no representatives of recent genera. These data should, however, be treated with a certain amount of caution. The Early Cretaceous Ichneumonidae including forms with the type of venation normal for that family, have not been studied as yet, and the Late Cretaceous forms have been derived from fossil resins of Taimyr, which enclose only small insects (commonly 2-3mm or less in size). Given this type of selection, Ichneumonidae with a much larger average size are naturally represented mainly by aberrant forms, while for Braconidae this size category is close to normal. This circumstance may also account for the considerably greater abundance of Braconidae in Cretaceous ambers; in the original fauna they may have been less numerous than Ichneumonidae.

Ichneumonidae and Braconidae are fairly similar from the ecological viewpoint. It is doubtful that the segregation of Braconidae was accompanied by drastic changes in their relationship with the host insects, but their transition to endoparasitism in the course of further evolution occurred on a much larger scale than among Ichneumonidae. Ectoparasitism persists only among Braconinae and in the subfamilies close to them, which form a diversified, but fairly well specialized group from the viewpoint of morphology.

Proctotrupoidea

The superfamilies Proctotrupoidea (including Diaprioidea, which are set apart in this work), Cynipoidea and Chalcidoidea are sometimes treated together under the name of Microhymenoptera. From the phylogenetic viewpoint this is, indeed, an integral group comprising predominantly small or very small insects. This group may have evolved as a consequence of miniaturization, as is evident not only from the reduction of venation in its members, but also from their remarkable parallelism with Braconidae in a number of characters. In addition to the broad costal area (a primitive character relative to Ichneumonoidea), a common feature of Microhymenoptera is their reduced venation (in extreme cases to one single short vein) and the presence of fewer hooklets which are more closely spaced and are displaced to the projection

of the anterior margin of the posterior wing (there are usually 2-3 hooklets, rarely 5-6, extremely rarely and probably secondarily up to 8, as in Pelecinus Latr.). Another common characteristic of the Microhymenoptera is the loss of the cocoon typical of Hymenoptera (according to Kochetova, 1966, Gilmour, 1970 and Vu Kuang Kong, 1974, the cocoons of Scelionidae and Chalcidoidea are of a different origin, hence secondary). Furthermore, the characteristic feature of the individuals with a relatively complete venation is the straightened out Cu (or at least the absence of the usual sharp bend backward in Cu at the point of the lm-cu junction). p.83

In addition to the characters listed above, the factors uniting Microhymenopera are some of their evolutionary tendencies: the decrease in the size of their labiomaxillary complex and oral opening accompanied by the appearance of the hypostomal bridge (see fig. 85f); the oligomerization of their antennae (polymerous antennae persist only in a few Jurassic Proctotrupoidea); the reduction of their abdominal spiracles (excepting the propodeal and the last, i.e. the seventh metasomal spiracles); the loss of the tooth-shaped condyles of the propodeum; the modification of the first metasomal segment to a slender and/or short articulation tube; the reduction of the cusps in the genitals of males; the displacement of the digiti to the aedeagus; shortening of the parameres (intergrown gonocoxae and gonostyles), which become intergrown with the aedeagus, as a result of which the main fixative function shifts from the parameres to the digiti and aedeagus; and the change-over to endoparasitism (ectoparasitism is known only among Chalcidae). Almost all these modifications are related to some degree to the decrease in the size of the insects; some of these changes, particularly those pertaining to the genitals and the mode of development, as well as those already discussed earlier (the reduction of venation and the structure of the apparatus holding the wings in place) have also been observed in Braconidae, particularly in their smaller representatives.

Judging from the broad costal area and from the persistance of the free postspiracular sclerite in some of their representatives, Microhymenoptera have originated from primitive forms unknown to us,rather than from typical Ichneumonoidea, where these characteristics are lacking. Since in some Ichneumonoidea the modifications of the head capsule are merely in the incipient stage and the postgenae are not yet completely forced apart by the lower tentorial bridge, we are compelled to assume that the separation of the postgenae occurred independently in Microhymenoptera and Ichneumonoidea. The resemblance of Microhymenoptera to Braconidae should also be regarded as a result of a parallel evolution. In the contrary event, if we assumed that this group descended from Braconidae, we would have to admit the possibility of the secondary appearance of the broad costal area, which practically disappeared in Ichneumonoidea, and of the restoration of the postspiracular sclerite, which has no external expression in the latter insects. Theoretically it would be possible if Ichneumonoidea retained in their ontogenesis the necessary prerequisites for these developments. So far, however, we don't know any other examples of the reversible reduction of the structures discussed.

The oldest and most primitive Microhymenoptera belong to Proctotrupoidea. This superfamily is given here a much narrower interpretation than usual for the following reasons. The differences between the "group Heloridae" instituted by Kozlov (1968) and the "group Diapriidae" appear to be much more profound than those between the latter group and Cynipoidea. In order

to treat Proctotrupoidea within their former limits we would have to add to them the gall wasps (Cynipidae), which is rather unwise. It appears more rational to set apart the "group Diapriidae" as the superfamily Diaprioidea.

Proctotrupoidea s.str., i.e. Mesoserphidae, Proctotrupidae, Heloridae and the groups close to them (figs 115-122), differ from the other Microhymenoptera in having identical antennae in both sexes, a short (no longer than twice its width) scape and commonly a long (covering more than one-third of the posterior wing) anal region in which the hind wing attains its maximum width. Furthermore, Proctotrupoidea retain the head structure and commonly the structure of the abdominal joint that are characteristic of Ichneumonidea; their 1+2r and 1mcu cellules are separated by RS+M, the pterostigma is present, and the assortment of their hosts is probably close to the original one (larvae of beetles, rarely larvae of Neuroptera and lower Hymenoptera, very rarely those of Diptera). In other superfamilies the antennae have a longer scape (except in some gall wasps, where the scapus is secondarily abbreviated) and the structure (often also the number) of the segments in the antennae is different in males and females; the anal lobe of the posterior wing is short and does not extend to the level of the greatest wing width; the ichneumonoid structure of the head and, often, of the abdominal joint is almost invariably lost (except in some Scelionidae); the 1+2r and 1mcu cellules are not separated; the pterostigma persists only in some Diapriodea (the "pterostigma" of the gall wasps from the subfamily Pycnostigmatinae is not homologous with the true pterostigma), and parasitism of the larvae of beetles appears to have been proven only for Chalcidae. p.85

All the Proctotrupoidea for which the pattern of development is described, are endoparasites, but since their probable descendants may include ectoparasites (many Chalcidae) and since their reversal from endo- to ectoparasitism has not been proven, we should assume that the primitive Proctotrupoidea, in particular Mesoserphidae of the type of Mesoserphus Kozlov

115-Mesoserphus sp., Upper Jurassic, Southern Kazakhstan; 16-Proctocyrtus jurassicus Rohd.; Upper Jurassic, Southern Kazakhstan; 117-Helorus rugosus Thom.; recent; 118-Ropronia garmani Ashm.; recent; 119-Iscopinus baissicus Kozl.; Lower Cretaceous, trans-Baykal region; 120-Pelecinopteron tubuliforme Brues.; Upper Oligocene, Baltic region; 121-Austroserphus sp.; recent; 122-Vanhornia euchnemidarum Crawf.; recent (115,116 and 119-originals; 115-Karatau, specimen PIN N° 2335/28; 116 and 119-holotype; 117 from Masner, 1957; 118-from Townes, 1948; 120-from Kozlov, 1974; 121-from Riek, 1970c; 122-from Handlirsch, 1925).

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The relationships and size of the constituent families of Proctotrupoidea are somewhat obscure. To a significant degree this is due to the fact that many Mesozoic Proctotrupoidea have been merely touched upon by research. A preliminary survey of this material shows that most of the Jurassic Proctotrupoidea form a spectrum bounded by the archaic Mesoserphus on the one hand and by the advanced Protohelorus Kozlov, Mesohelorus Mart. and Protocyrtus Rohdendorf on the other (see fig. 116). Mesoserpus have a long soft metasoma with an external ovipositor, an apically broad 1r (basal) cellule and narrow slender cubitoanal cellules in their anterior wing, while the other forms have a rigid oval metasoma, where the first cylindrical segment may even be segregated, though is not as narrow as in Helorus Latr. (see fig. 117). Ovipositor hidden, cellule 1r in the anterior wing narrow, cua very broad. These forms already resemble Helorus very closely, sometimes to the point of displaying a secondary crescent-shaped vein near the postero-outer corner of the cellule 2cua, and the Late Cretaceous forms from Bon-Tsagan in Mongolia fill to a significant extent the remaining part of the hiatus. The forms intermediate between Mesoserphus and Proctohelorus are proctotrupoids with an external ovipositor and a venation pattern similar to that of Mesoserphus; they are very small, with a rounded metasoma, or medium-size, with a rigid, more or less cylindrical metasoma.

Even these preliminary data reveal the roots of the family Heloridae. It may be advisable to include into this family Mesohelorus, Protohelorus, Protocyrtus and the forms close to them with the rank of a subfamily referred to as Protohelorinae A. Rasnitsyn, subfam. nov. (the other types of Jurassic proctotrupoids mentioned earlier are tentatively referred to the family Mesosephidae and await description from the systematic viewpoint). A more thorough study may also enable us to discover the roots of the other families of Proctotrupoidea.

Of the four remaining families Roproniidae with their petiolate, as in Heloridae, but laterally compressed and less markedly sclerotized metasoma, their hidden ovipositor and less primitive venation than that of Heloridae, are similar in many respects to the latter family, but their parallel and independent evolution from some mesoserphids is equally possible.

The families Proctotrupidae, Vanhorniidae and Pelecinidae, parasitize almost exclusively the larvae of beetles (unlike Helorus and Ropronia developing on the larvae of Neuroptera and Tenthredinidae, respectively). In addition to this they are united by their annular pronotum that has also been observed among Microhymenoptera in Scelionidae and Platygastridae. In all these groups the ring appears to arise as a result of the intergrowth of the pronotum with the hypertrophied and medially intergrown postspiracular sclerites (fig. 123). These sclerites are probably homologous with the primary basalare* of the lower Hymenoptera and are highly characteristic of Stephanidae and many Aculeata, where they may also coalesce forming a half-ring (in many Bethyloidea); they are also present in Chalcidoidea, but this will be discussed later on. The early developmental stage of the ring may be observed in Monomachidae, where sclerites are not even in contact yet, are distinctly separated from the mesothorax and are partly

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* Transliteration. Unable to find the English equivalent. Translator.

covered by the posterior margins of the pronotum, with which they only begin to intergrow. A later developmental stage can be observed in Vanhornia Craft. and in some Scelionidae (the tribe Caloteleini): the ring is present, but the boundary between the pronotum as such and the postspiracular sclerite intergrown with its posterior margin is clearly defined, and the sclerite itself is broad and oval. With further development (in Proctotrupidae, Pelecinidae, Platygastridae and in most Scelionidae) the sclerite loses its distinctly segregated character. Moreover, Proctotrupidae and Pelecinidae acquire an additional feature in common, an unusual position of the mesothoracic spiracle that is displaced onto the lateral surface of the pronotum (which appears to be clamped between this surface and the upper portion of the post-spiracular sclerite, the boundary between which is still discernible in Pelecinidae). In addition to this the two families are united by their extensive parasitism of the larvae of edaphic beetles and by the tendency of their metasoma to become elongated. p.86

The Early Cretaceous Iscopinus Kozl. (fig. 119) belonging to Pelecinidae (Kozlov, 1974), is the form with the most primitive structure in this group. It retains characters of the kind of multi-segmented (probably 18-segmented) antennae, normal mandibulae with three or more denticles, occipital crest, well-developed notaulae that do not merge posteriorly, a virtually unmodified (only slightly stretched) abdomen with homonomous segments, and the case of the ovipositor that does not protrude above the top of the abdomen. Its posterior wings are, however, already free of distinctly defined venation, similarly to those of the other Pelecinidae, Proctotrupidae and Vanhorniidae. The additional vein "RS_2" (Kozlov, 1974, marked it as 2r-m), which was used as a criterion in referring Iscopinus to Pelecinidae, still resembles more closely that vein in some of the Proctotrupidae forms (fig. 124a). The vein in question seems to be a secondary formation appearing independently in many Hymenoptera. It may be very similar in position and shape to RS which persists in some Symphyta (see figs 41-42). The secondary "RS_2" is characteristic of Pelecinidae, Multillidae, Plumariidae (see figs 120, 148 and

189-190) and of some Chrysididae; its vestiges may also be observed in Scelionidae (Macroteleia Westw.) and in some Chalcidae, particularly in the forms that have secondarily increased in stature (it is most clearly observable in Leucospis F.). Moreover, the secondary nature of RS_2 is clearly perceptible in Pseudophotopsis André, one of the most primitive Mutillidae: this vein intersects here 3r-m and penetrates inside the 3rm cellule (fig.124b). "RS_2" in the form of a short process on 3r-m is considerably more wide-spread (in some Pergidae and Braconidae, among the ants in Myrmecia, etc.).

The features of Iscopinus characteristic of Pelecinidae are the elongation of their abdomen (though it is still rather weakly defined) and their short ovipositor. The features distinguishing it from Pelecinus Latr. and Pelecinopteron Brues., first of all the differences in the structure of their abdomen and in the shape of the "RS_2" discussed above, are, however, so serious that we are compelled to set this genus apart as a separate subfamily Iscopininae A.Rasnitsyn, subfam. nov. (the nominal subfamily Pelecininae Halidae 1840, stat. nov. is composed of Pelecinus and Pelecinopteron).

The difficulty regarding the relationship between Pelecinidae, Proctotrupidae and Vanhorniidae lies in the differences between the apomorphic features distinguishing Proctotrupidae from Pelecinidae (the position of the first thoracic spiracle and the tendency to form "RS_2") on the one hand and those separating them from Vanhorniidae (such as the disproportionately enlarged first segment of their metasoma and the distinctive structure of their ovipositor, which should be discussed in greater detail; see fig. 125) on the other. The third valves of the ovipositor are modified here (as is also the case in the mecopteroids, neuropteroids and beetles) from a case to a functional part of the ovipositor and actively penetrate into the substratum. As a result of the distal displacement of the basal joint of the second valves the ovipositor can bend downwards without dragging along the apex of the last abdominal sternite, the margins of which remain firmly appressed to

the margins of the apical tergites. This means that in the ancestors of these two groups the apex of the abdomen was tightly closed and the ovipositor was retracted, as is the case in nearly all the forms of Proctotrupoidea and Diaprioidea; consequently, the external ovipositor of Proctotrupidae and Vanhornia is secondary. The structure of the ovipositor in Diapriidae is an additional argument in favour of that hypothesis. In repose their ovipositor is retracted into the abdomen and its third valves resemble, at least superficially, stylets rather than a case (they are slender, glossy and nearly glabrous with a mere few setae at the top).

Figs. 123-125 p.87

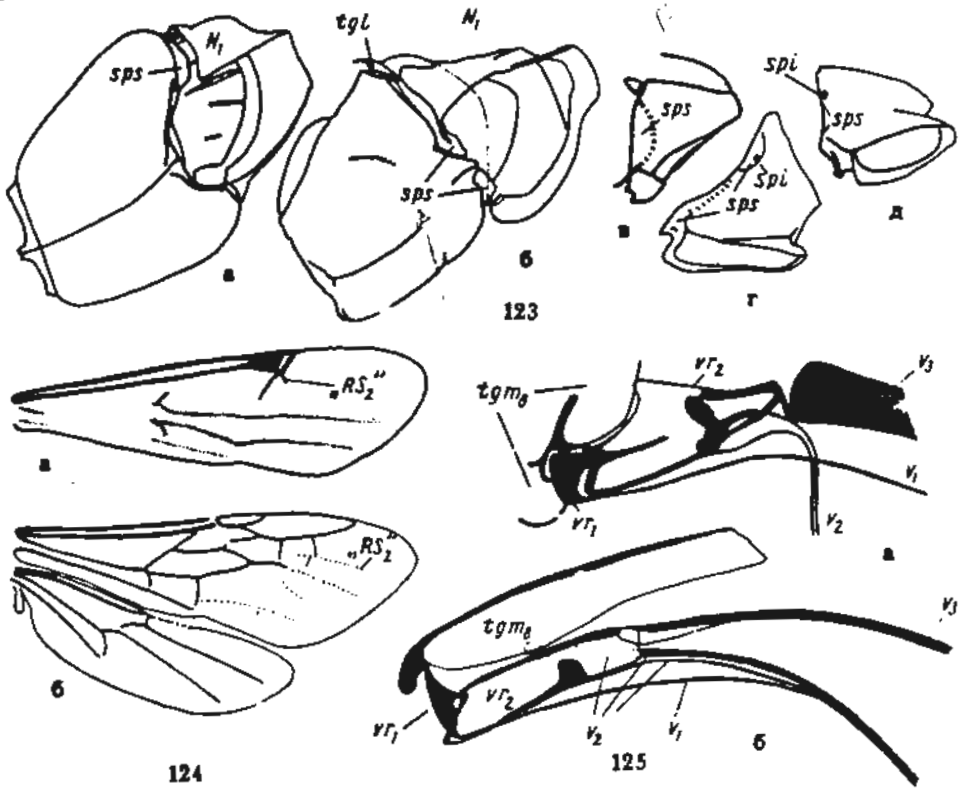

Fig. 123
Postspiracular sclerite
a-Schlettererius cinctipes (Cress.), Stephanidae; b-Monomachus sp., Monomachidae; c-Caloteleia sp., Scelionidae; d-Pelecinus polyturator (Drury), Pelecinidae; e-Proctotrupes gladiator Hal., Proctotrupidae (all of them recent, originals).

Fig. 124
Anterior wing: a-Proctotrupes gladiator Hal. (Proctotrupidae), b-Pseudophotopsis sp. (Mutillidae) (recent, original).

Fig. 125
Ovipositor
a-Proctotrupes gravidator L., b-Vanhornia eucnemidarum Crawf. (recent, originals).

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The third valves of many Proctotrupidae, unlike those of Vanhorniidae, are still very similar to a protective case, even though their function has been modified, and the segments of their metasoma may be very markedly elongated (Riek, 1955a, fig. 4), even though they are still capable of telescopic retraction. The elongation of these segments for the purpose of enabling the metasoma to penetrate into the substratum after the ovipositor, if the insects parasitized live in the soil, is distinctly parallel to the evolutionary trend of the metasoma in Pelecinidae. However, the ovipositor in Pelecinus has a totally different structure: it is concealed, abbreviated and somewhat reduced; in particular the basal joint of the second valves is lost in it; the third valves act as a protective case, but are fairly specific because of the presence of large sensory fields at their apices.

Among the characters described the most important ones (that have not been encountered in any of the other Hymenoptera and appear to be less susceptible/parallel development than the others) are the structure of the ovipositor and the disposition of the spiracle on the surface of the pronotum. However, the distribution of these characters contradicts the hypothesis of their having occurred simultaneously; we are compelled to admit the possibility that at least one of these characters arose independently. Since the morphological modifications are less profound, it appears more probable that the second characteristic

(the position of the spiracle) is a parallel development. This suggests that Proctotrupidae are close to Vanhorniidae and that both have descended from Pelecinidae which are close to Iscopininae. This may also be inferred from the close resemblance of Vanhorniidae and Proctotrupidae not only with regard to their basic general organization, but also in many structural details of their ovipositor. p.88

Of the six families of Proctotrupoidea the family Mesoserphidae was the most abundant and varied one in the Jurassic times (large quantities of their remains have been derived from the Upper Jurassic deposits of Karatau in Southern Kazakhstan; moreover, their remains are known from the Middle or Upper Jurassic on the Uda river in the trans-Baykal region and from the Lower-Middle Jurassic at Beibyao in Eastern China) and survived until the Early Cretaceous (Baisa in the trans-Baykal region and Bon-Tsagan in Mongolia). Heloridae are common in the Late Jurassic of Kazakhstan (Karatau) and in the Early Cretaceous of Mongolia (Bon-Tsagan); moreover, they have also been found in the Late Oligocene (the genus Helorus in Rotte*, FRG). Roporoniidae are unknown in fossil state. Proctotrupidae appear in the Early Cretaceous of the trans-Baykal region (Baisa) and Mongolia (Bon-Tsagan) and are known from a number of later Paleogene deposits, beginning with the Paleocene of Primor'e (Zerkal'naya). Pelecinidae have also been recorded since the Early Cretaceous (Iscopininae in the trans-Baykal region and Pelecininae in Bon-Tsagan from Mongolia); later on Pelecininae were found in Baltic amber of the Eocene age and in the amber from Sakhalin, the exact age of which within the Paleogene has not been determined. Fossil Vanhorniidae are unknown. Proctotrupidae and Heloridae alone are widely distributed among the recent fauna; Pelecinidae are confined to the New World, Roproniidae to the Nearctic and Eastern Palearctic regions, and Vanhorniidae to the Nearctic regions.

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* Transliteration. Translator.

Diaprioidea

The superfamily Diaprioidea (figs 126-134) is characterized first of all by antennae with an elongated scape and with sexual dimorphism in the number of segments and structure of the antennae (clavate in females, filiform in males). In the anterior wing RS+M is lacking between the 1+2r and 1 mcu cellules even in forms with a relatively complete venation. The posterior wing has a short anal lobe and is expanded far beyond its apex (except in Austronia Riek). Head capsule only in Ismarus Hal. (Diapriidae) with hypostomes that are not in contact (the structure of this region of the head in Austroniidae is not known). Propodeal opening almost invariably free of denticles. A very characteristic feature is the development of these insects in larvae and puparia of Diptera and their eventual parasitism of eggs via the morphotypical specialization (i.e. modification of their specialization for hosts within the limits circumscribed by the habitual similarity of the victims; Kozlov, 1970, 1972) (see Kozlov, 1968); Diaprioidea parasitize other hosts very rarely and when they do so, it is almost certainly a secondary development.

The superfamily Diapioidea comprises the families Austroniidae (including Trupochalcididae), Monomachidae, Diapriidae, Platygastridae, Scelionidae, Serphitidae (including Mymarommatidae) and Myramidae. Compared to the "group Diapriidae" (Kozlov, 1968), the composition of this superfamily is enlarged on account of Austroniidae, Myramidae and Mymarommatidae (which is here a subfamily of Serphitidae). The first family has been referred by Kozlov (1968) to the "group Heloridae" and the two last families are commonly amalgamated and included into Chalcidoidea. The criteria on the basis of which Austroniidae are referred to Diopriidae are the sex dimorphism in the structure of their antennae (established only in Austronia) and the structural similarity of their thorax to that of Monomachidae. The attributes characteristic of the Late Cretaceous Microserphites A.Rasn. (Kozlov, Rasnitsyn, 1979) and Distylopus Yoshimoto corroborate the closeness of

Mymarommatinae to Serphitinae. Distylopus Yoshimoto has been described as a separate subfamily Distylopinae among the chalcids of the family Tetracampidae (Yoshimoto, 1975), but it is more probable that this form belongs to Serphitidae.

The taxonomic position of Mymaridae has always been somewhat obscure and is intermediate between Chalcidoidea and Proctotrupoidea (Debauche, 1948; Nikol'skaya, 1952). Some of the most important diagnostic characteristics of Mymaridae appear to be variable: their pronotum may or may not extend as far as the tegulae, the postspiracular sclerite may be present or absent, or it may look like a part of the mesopleuron separated by an incomplete incision. It may indeed be a secondary formation that is not homologous with the true postspiracular sclerite. p.89

The other characters of Mymaridae suggest contradictory conclusions regarding their relationships and are for the most part equally unreliable. For example, the absence of ringlets (i.e. small segments at the base of the flagellum of the antenna) forms a link between Mymaridae and Diaprioidea, but the ringlets may also be lacking in the chalcids (such as Chalcididae Leucospidinae). On the other hand the incompletely closed apex of the metasoma in the females and the more or less external position of the ovipositor are characteristic of both Mymaridae and Chalcidae, but there is even a group of Diaprioidea (Serphitidae, particularly Mymarommatinae) among which the gaping apex of the metasoma and the external position of the ovipositor are fairly common features. Sensory crests on the antennae are characteristic of Mymaridae and Chalcidae, but not of Diaprioidea. Typical sensory crests are unknown in the other Diaprioidea, but their presence in gall wasps shows that these formations may appear independently if not in Diaprioidea themselves, then at least in their descendants. The early stages of formation of the sensory crests have apparently also been observed in some representatives of Diaprioidea. For example, the distal segments of the antennae in Trupochalcis definitely bear large elongated-oval sensillae. Other structures which may resemble precursors of the sensory

crests even more closely, are developed on the distal segments of the antennae in some forms of Mymarommatinae, a group that evolved parallel to Mymaridae in many of its characteristics. In some of the Late Cretaceous Mymarommatinae, in addition to the common pili, these segments bear thicker hairs sharply bent at the base and extending farther on close to the surface of the segment and parallel to its axis; in that event the adaxial side of the hairs displays a rudimentary membranous crest (Kozlov, Rasnitsyn, 1979). It is easy to visualize the transformation of such a hair into a sensory crest as a result of its adgrowing to the segment.

It would appear that the most reliable indications of the relationships of Mymaridae may be derived from the structure of their larvae that are of the same rather distinctive type as the larvae of Scelionidae (Nikol'skaya, 1952). This circumstance, combined with the major structural characters of the postspiracular sclerite in Mymaridae and with the multitude of their parallelisms with Mymarommatinae, suggests that Mymaridae should be transferred to Diaprioidea and be placed close to Scelionidae and Serphitidae.

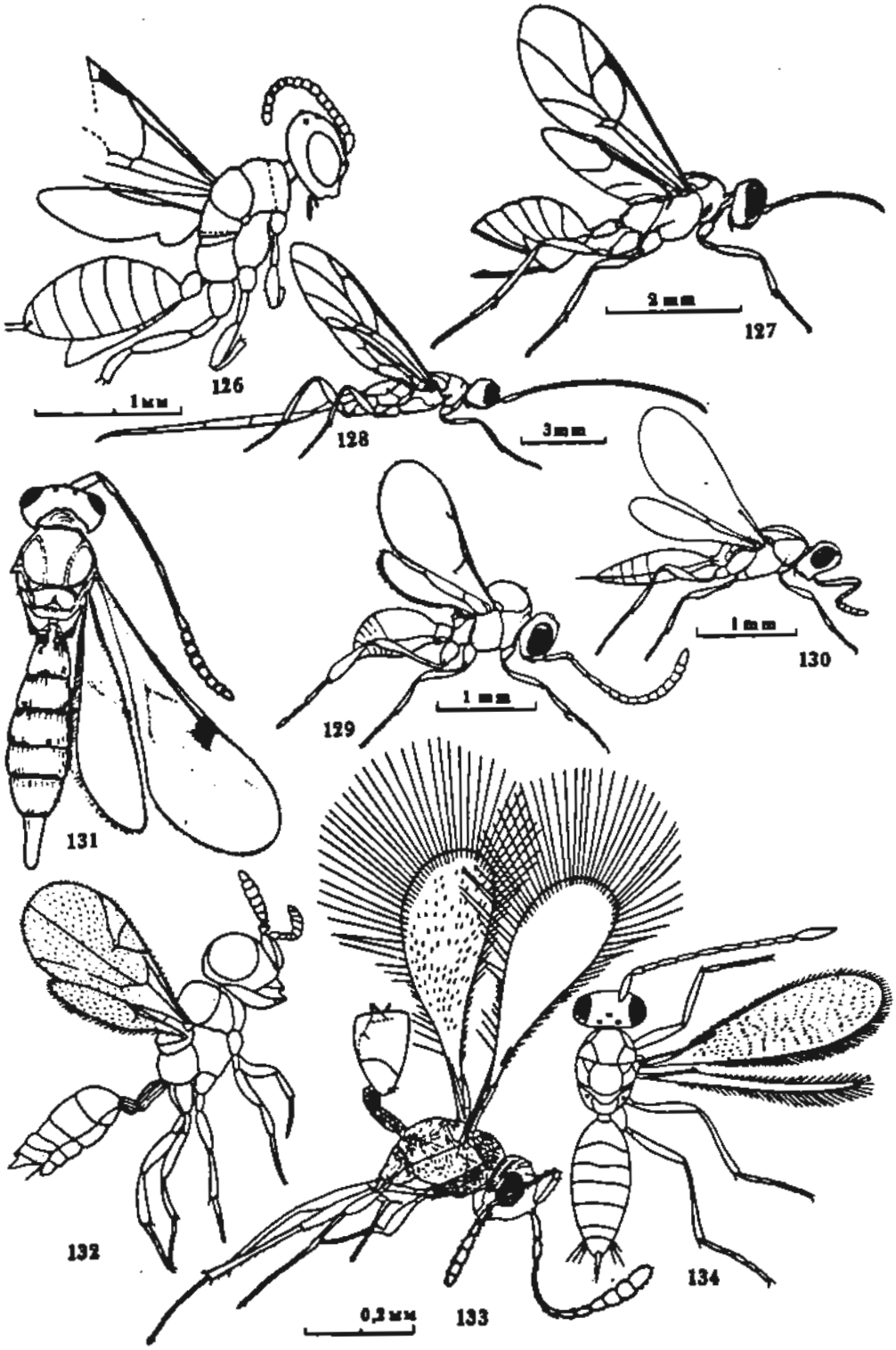
The relatively short C-shaped r-m of the posterior wing and the primitive structure of the metasoma and ovipositor in Austroniidae suggest that Diaprioidea descended from Mesoserphidae that were similar to their so far undescribed representatives from the Middle or Late Jurassic of the trans-Baykal region (Uda) and from the Early Cretaceous of Mongolia (Bon-Tsagan).

Austroniidae is the most primitive family of Diaprioidea with regard to most of its characters. It is composed of two monotypical subfamilies: Austroniinae with the recent genus Austronia Riek (Riek, 1955b, 1970b) and Trupochalcidinae which includes Trupochalcis Kozl. from the Late Cretaceous deposits of Taimyr (Kozlov, 1975). Trupochalcis was classified in its description as a separate family Trupochalcididae similar to Austroniidae, but the differences between them appear to be on the level of a subfamily rather than of a family. The primitive external ovipositor, the gaping apex of the metasoma, the outer

external rod-shaped cerci, the primitive structure of the wings, particularly in Austronia, the posterior wings of which do not taper towards the base, are the characters persisting in Austroniidae. Venation of the wings, of the hind wings in particular, is somewhat less complete in Austroniidae than in Monomachidae. Their advanced characters include first of all the short and narrow tubular shape of their first metasomal segment exhibiting no traces of the boundary between the tergite and sternite, and, secondly, their narrow and relatively long pronotum with its tapered posterior corners stretched backwards and laterally (towards the tegula). This has been established with confidence in Trupochalcis, but Austronia also has at least the stretched-out posterior corners. Kozlov's report (1973) regarding the existence of a form intermediate between Proctotrupoidea and chalcids among the fauna of the Upper Cretaceous ambers from Taimyr, refers precisely to Trupochalcis and is based on the primitive structure of the metasoma and on the shape of the pronotum in that insect. Austronia and Monomachidae are, however, characterized by a similar structure of the pronotum and, in addition to that, the latter forms have free postspiracular sclerites that are typical of the chalcids (fig. 123b). On the other hand it is entirely possible that these sclerites are also free in Austroniidae. The relationships of Chalcidoidea are discussed in greater detail farther on. p.91

As may be seen from the above, Monomachidae, representatives of which are widely distributed in Australia and South America (but are not found in fossil state), are a primitive group close to Austroniidae. The resemblance between the two families is reinforced by the tubular first metasomal segment of Monomachidae, although it is long and exhibits a perceptible vestige of the boundary between the tergite and sternite. The tubular segment is also characteristic of Diapriidae, where it is, however, commonly costate and more massive. A closer type of the first segment of the metasoma forming a slender smooth tube, has been encountered among Serphitidae and Mymaridae, but in this instance its independent development is beyond doubt.

Figs. 126-134



Representatives of the superfamily Diaprioidea
126-Trupochalcis inops Kozl.; Upper Cretaceous of Taimyr, Austroniidae Trupochalcidinae; 127-Austronia sp.; recent; Austroniinae; 128-Monomachus sp.; recent; Monomachidae; 129-

Ismarus sp.; recent; Diapriidae; 130-Brachinostemma sp.; recent; Platygastridae; 131-Archaeoteleia novozelandiae Masner; recent; Scelionidae; 132-Serphites dux Kozlov; Upper Cretaceous of Taimyr; Serphitidae Serphitinae; 133-Palaeomymar agapa A.Rasn.; Upper Cretaceous of Taimyr; Serphitidae Mymarommatinae; 134-Gonatocerus cicadellae Nik.; recent; Mymaridae (126-from Kozlov, 1975; 127 to 130-from Riek, 1970b; 131-from Masner, 1968; 132-133- from Kozlov, Rasnitsyn, 1977; 134-from Nikol'skaya, 1952).

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Diapriidae, the largest and most widely distributed group within the superfamily, are fairly close to Monomachidae and Austroniidae. Diapriidae are characterized by a commonly tumid and elongated face (excepting some as yet undescribed Late Cretaceous forms; M.A. Kozlov, personal communication), a venation that is somewhat more markedly reduced than that of Austroniidae and Monomachidae, the lack of the pterostigma and the presence of one (3r) or, less often, two (1rm and 3r) closed cellules in the anterior wing; a usually thick and costate first metasomal segment that has a circular cross-section and no distinct boundary between the tergite and sternite; a normal metasoma that is not as markedly elongated as that of Monomachidae, has a closed apex and a retracted ovipositor in the state of rest.

Scelionidae, another large family of Diaprioidea, is segregated from the three preceding families much more markedly. Scelionidae are characterized by a transverse scutellum that is markedly expanded laterally and commonly is not separated anteriorly by a deep and broad depression (in the first three families the scutellum is narrow, bearing anteriorly a deep depression often separated in the middle); pronotum annular; metasoma commonly with sharply segregated laterotergites forming a sharp angle with the tergites (among the Diaprioidea discussed this character has been observed only in Ambositrinae, a small and fairly advanced subfamily of Diapriidae); a normal (not tubular) first segment; the second tergite of the metasoma may not be enlarged relative

to the next tergites, as is characteristic of Diapriidae (except of some Late Cretaceous Diapriidae that have not been described as yet); in male genitals the gonostyles are markedly reduced and the digiti are adgrown to the aedeagus, as is also the case in Chalcididae, but the basal ring persists, unlike that of Chalcididae. In contrast to Diapriidae, which commonly develop in larvae and puparia of Diptera, all the Scelionidae are egg parasites.

M.A. Kozlov believes (1968 and a personal communication) that Scelionidae have descended from primitive Diapriidae and that the intermediate stages of that process are illustrated by the as yet undescribed Diaprioidea found in the Late Cretaceous (Santonian) resins from Yantardakh in Taimyr. Serphitidae and Mymaridae are among the probable descendants of Scelionidae. Both families lost the ring-shaped pronotum, more or less closed apex of the metasoma and retractable ovipositor (this is less pronounced in Serphitinae). Both are characterized by a tendency to an extreme miniaturization, reduction of venation (to the point of losing the whole lamina of the posterior wing in Mymarommatinae and Mymar Curtis) and development of a long fringe along the edge of the wing, to lodging the mesopleuron between the pronotum and tegula, and to the modification of the first (in Serphitidae of the two first) metasomal segments to an articulated tube. These two families are not derived directly from one another, since Serphitinae, which inherited from Scelionidae a multitude of their characters, have at the same time a two-segmented petiole, p.92 which also persists in Mymarommatinae. On the other hand Mymaridae inherited the primarily unmodified structure of the base of the metasoma and differ from Scelionidae in other characteristics that are often similar to those of Mymarommatinae (in the structure of their antennae, thorax, wings and apex of the metasoma, including the position of their ovipositor, etc.). Mymaridae and Serphitidae appear to have diverged off Scelionidae independently and, probably, at a different time: Serphitidae are found in the paleontological record since the beginning of the Cretaceous (in the Neocome) and Mymaridae only since the

beginning of the Late Cretaceous and occur there considerably less often than Serphitidae, particularly Mymarommatinae .

Platygastridae, the last family of Diapioidea, is just as large as Scelionidae and is only smaller in size than Diapriidae and Mymaridae. A few of its essentially primitive characters (the structure of its pronotum, its enlarged second tergite and its parasitism of Diptera larvae) from a link between that family and Diapriidae. On the other hand Platygastridae have both synapomorphic features (general specializations) (the annular pronotum and the male genitals reduced in a similar manner) and symplesiomorphous characters (the first metasomal segment is distinctly divided into a tergite and a sternite and still resembles the first segment rather than the articulation tube of Diapriidae, in spite of its having been modified more markedly along the lines of an articulation tube) in common with Scelionidae. The young larvae of both families are markedly juvenilized, but with different results in their organization, which may testify rather against a close relationship between Platygastridae and Scelionidae. According to M.A. Kozlov (1968 and personal communication) the resemblance of Platygastridae to Scelionidae is largely of a secondary nature and the former family is genetically related directly to Diapriidae.

The paleontological history of Diaprioidea begins in the Early Cretaceous. A remain of a Serphitidae (Serphitinae) form was found in the Neocomian of the trans-Baykal region (Baisa), and remains of Scelionidae and, presumably, Serphitidae have been discovered in the Upper Neocomian or Aptian of Mongolia (Bon-Tsagan). In the middle of the Cretaceous Mymarommatinae made their appearance and Scelionidae became abundant (the Taimyr localities of Kresty and Bediei and the Agdzhakent locality in the trans-Caucasus). Scelionidae and Mymarommatinae remained abundant throughout the Late Cretaceous, while the abundance of Serphitinae first increased towards the Santonian, then declined once again towards the Campanian. Mymaridae appeared at the beginning of the Late Cretaceous (the Late Cenomanian of Taimyr, Agapa), but

their abundance and diversity had not reached high indices as yet. Diapriidae are known since the Turonian (Timmerdyakh-Khaya in Yakutia) and Platygastridae only since the Paleogene (the Eocene Baltic amber and the amber from Sakhalin, the age of which within the Danian- Eocene time-interval has not been determined). So far only a small portion of fossil Diaprioidea has been described (for the Cretaceous, see Brues, 1937; Yoshimoto, 1975; Kozlov and Rasnitsyn, 1979; the data on the Cenozoic have been summarized by Zherkhin, 1978).

Cynipoidea

Gall wasps (the superfamily Cynipoidea) (figs 135-141) are very similar from the morphological and biological viewpoints to Diaprioidea, particularly to Diapriidae and Austroniidae, and descended probably from some forms close to the latter. Antennae with no more than 15 segments*, with a structure exhibiting signs of sexual dimorphism similar to those recorded in Diaprioidea; these characters include even incisions on the basal segments of the flagellum that are characteristic of Diapriidae. Scapus often elongated, particularly in more primitive groups (among Figitidae and Ibaliidae, s.l.). However, in contrast to most Diaprioidea (with the exception of Mymaridae), in gall wasps the segments of the antennae are furnished with sensillae. The antennae are attached here, similarly to those of Diaprioidea, high above the clypeus, but the face is not tumid. Another highly characteristic feature of these insects is the stable shape of their head, which is broad, tapering downwards, commonly with short and broad closely spaced mandibulae and a small clypeus. In contrast to p.94
Diaprioidea, where the hypostomes are completely separated by the lower tentorial bridge only in Ismarus, this rather primitive structure of the head capsule is wide-spread among these forms, although the hypostomal bridge may also be very similar in appearance to the postgenal bridge (see fig. 85f).

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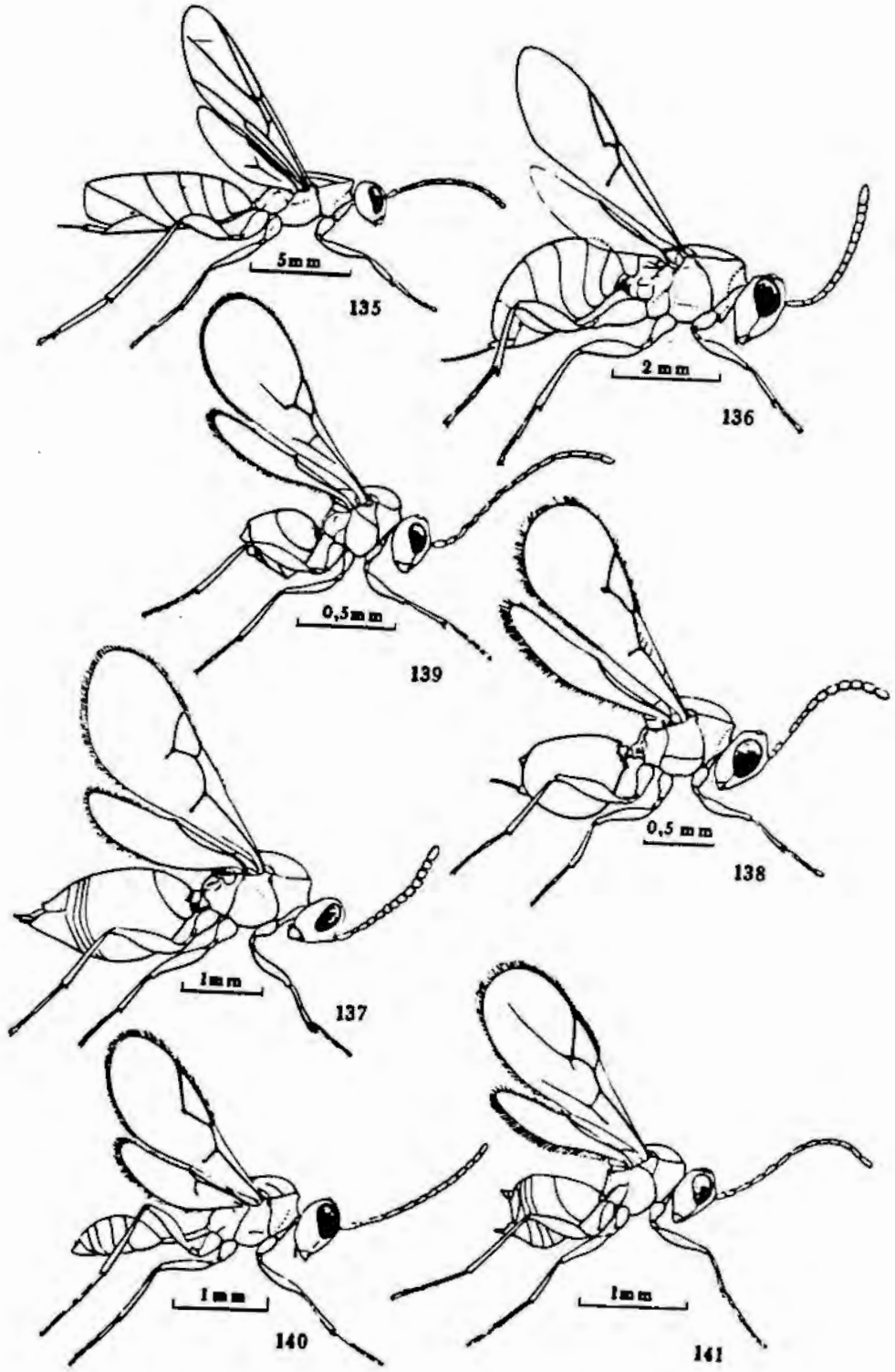
* In Pycnostigmatinae the females have 12-19 and the males 15-24 segments of the antennae; this appears to be a secondary modification.

Figs. 135-141



Representatives of the superfamily Cynipoidea (all recent)
135-Ibalia sp., Ibaliidae Ibaliinae; 136-Mesocynips sp., Ibaliidae Mesocynipinae; 137-Xyalophora sp., Figitidae Figitinae; 138-Heptamerocera

sp., Figitidae Eucolinae; 139-Charips australiae, Figitidae Charipinae; 140-Anacharis sp., Figitidae Anacharitinae; 141-Aylax hypochoeridis Kieff., Cynipidae (from Riek, 1970b).

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The structure of the thorax in Cynipoidea and Diapriidae is similar in a number of characters, including their markedly reduced propodeum, even though this feature is characteristic only of some Diapriidae (and, to a lesser degree, of Trupochalcis). Many Cynipoidea have a median suture of the mesonotum, a feature unknown in Diaprioidea and generally rare among Ichneumonomorpha. It seems to appear here and in the other representatives of the infraorder secondarily, as a means of reinforcing the boundary between the two powerful dorsovental muscles of the thorax. In any event it is lacking in more primitive forms (most Figitidae and Ibaliidae Mesocynipinae) and is observable there only in the form of an incipient depression or a short longitudinal indentation anteriorly of the scutellum.

The structure of the wings is similar in many respects to that of many Diapriidae (including the shape and venation of the hind wing), but has also a number of specific characters. The radial cellule is for the most part markedly enlarged (its primitive form persists in many Ibaliidae). In most Cynipoidea the composite vein 1m-cu+RS bounding exteriorly the central cellule in Austronia and Monomachus, is displaced anterobasally with its lower end and extends roughly parallel to the axis of the wing; this displacement can, however, be already observed in its incipient form in Austronia. The most important characteristic of the wings in Cynipoidea is the presence in many of them of an areola, a cellule corresponding in shape and position to the areolet (2+3rm) of Ichneumonidae. This cellule is lacking in the other Microhymenoptera. The assumption that it is invariably present in the succession of ancestors of Cynipoidea implying the divergence of that superfamily off the forms that are even more primitive than Mesoserphidae, contradicts both their marked resemblance to Diaprioidea, which descended from Mesoserphidae,

and the later appearance of Cynipoidea that are known since the Late Cretaceous. Apparently the areola developed secondarily in Cynipoidea. This may also be inferred from its absence in Ibaliidae, a group that is primitive in many respects. In Kozlov's view expressed in conversation with the author of this work, the areola may have been closed secondarily by the vein (RS_2) developed in some Proctotrupidae. Another possible and more unconventional explanation is suggested by the venation of Mesocynips Cam., a fairly primitive Cynipoidea (table III, fig. 9). In this insect the vein bounding the central cellule is fully sclerotized only over the short segment underneath the corner of the radial cellule, but farther on it is sharply bent and reduced (weaker). The sclerotized segment is surrounded by a ⊓-shaped secondary thickening that is distinctly separated from the membrane and has the appearance of a true vein that is weak relative to the segment which it surrounds, but stronger than the vein adjoining it proximally. It is easy to visualize the appearance of the areola as a result of the membranization of the area bounded by the secondary vein, or as a consequence of the displacement of the proximal segment of the latter and eventual coalescence of its distal segment with the primary vein. The hypothesis regarding the disposition of the true vein along the outer edge of the areola stems from the fact that the outer vein of the areola is more stable and often remains sclerotized even after the reduction (desclerotization) of the inner vein.

The metasoma is commonly highly variable in Cynipoidea. Its first segment is modified to an articulation tube or ring without any boundary between the tergite and sternite, as is the case in many Diaprioidea. But, unlike that segment in the latter superfamily, it is often very short here and firmly adgrows to the second segment (in other cases it can be very similar to the petiole of Austroniidae and, particularly, of Monomachidae, such as the Anacharis Dalm., or Diapriidae, such as Paramblynotus Cam.). The metasoma is more or less compressed laterally in its major part, sometimes to the point of being foliate or cultellate in shape, but often merely to the extent of having an oval cross

section. Another characteristic tendency is towards disturbed proportions of the segments. Judging from Ichneumonoidea, in the least markedly modified metasoma of Ichneumonomorpha, particularly in that of the females, the segments, beginning with the second segment, gradually and more or less uniformly decrease in length towards the apex. Apparently this phenomenon has not been observed in any Cynipoidea, but virtually unaltered p.95
proportions of tergites are a feature characteristic of some Cynipinae (for example, in the genus Isocolus Förster). In most females of Cynipoidea the sternites are essentially proportioned similarly to those of Trupochalcis (their outer parts decrease from the second to the fifth sternite, while the sixth sternite is markedly elongated). In the females of Anacharis Dalm. they are nearly homonomous and even the sixth sternite is relatively little enlarged (and is approximately equal in length to the two preceding ones taken together). Furthermore, the sternites of Anacharis are moderately convex instead of being sharply bent along the median line, as is the case in female representatives of the other Cynipoidea.

The proportions of the tergites are an important taxonomic character in Cynipoidea. A more or less marked enlargement of the second (first after the stalk) tergite is believed to be characteristic of Cynipinae, Charipinae, Eucoilinae, Pycnostigmatinae and of most Anacharitinae. In reality it is also at least a little longer than any of the successive tergites in the other groups; moreover, this feature is characteristic not only of males, but also of females. For example, a characteristic attribute of Figitinae is that their third tergite is the longest one, whereas in Ibaliidae it is commonly the sixth, less often the fourth or the fifth tergite. However, in the females of Sarothrus (Amblynotus) opacus Hart. (Figitinae) and Kiefferiella rugosa Ashm. (Mesocynipinae) the second tergite is the longest. On the other hand in Charipinae the second tergite is practically no longer than the third one. In Eucoilinae and Pycnostigmatinae the "second" tergite, judging from the number of the tergites following it, is composed of the fused second and third tergites

in males and second-fourth tergites in females (the fused second and third tergites also characteristic of some Cynipinae, where there is, however, no sexual dimorphism with regard to that character). Furthermore, in most of the constituent groups of Cynipoidea the seventh tergite is more or less enlarged, more or less sharply downcurved together with several preceding tergites, and almost perpendicular to the axis of the metasoma (it is least of all characteristic of Cynipinae). The apex of the metasoma may be gaping or closed in Cynipoidea, but in the latter event it is not closed as tightly as in most Diaprioidea.

Most Cynpoidea have a distinctive structure of the ovipositor with the second valvifer curved in the form of a nearly complete ring so that its tips are oriented in the same direction and are almost on the same level. The ovipositor of Anacharitinae (Anacharis sp.), Figitinae (Sarothrus opacus) and Cynipinae (Adleria caput-medusae Hart., see Jonescu, 1957, fig. 15a) is, however, quite normal or (as in Adleria) only slightly modified.

The larvae of many Cynipoidea, particularly their young larvae, are characterized by the reactivation of rudimentary limbs on the thoracic and abdominal segments with formation of fleshy processes, i.e. pseudopods similar to those observed in Proctotrupidae and Heloridae (Clausen, 1962). There have been encountered no Diaprioidea larvae with pseudopods, but the group of their families that is closest to Cynipoidea (Diapriidae, Monomachidae and Austroniidae) has been little studied in that respect.

All the Cynipoidea, with the exception of their gall-forming representatives and of the inquilines inhabiting the galls, which constitute the subfamily Cynipinae, are endoparasites parasitizing the larvae and puparia of Diptera (Figitinae, Aspiceratinae and Eucoilinae); Ibalia are associated with Siricidae, Anacharitinae with Neuroptera, Charipinae are hyperparasites of the aphids infested by Braconidae of the subfamily Aphidiinae. Mesocynipinae probably develop in larvae of xylophagous insects (Weld, 1952).

If we sum up all the known primitive characteristics of Cynipoidea (the antennae with a long scape, 14- to 15-segmented antennae in males and 13-segmented ones in females, the pronotum without a median suture, the venation of the wings as complete as that of Mesocynipinae, the shape of the radial cellule and the absence of the areola, the shape of the central cellule as in Figitinae, the first segment of the metasoma as in Paramblynotus or in Anacharitinae, with a short petiole of the type found in Aegilips Wilkr., 2-8 tergites as in Isocolus, the sternites as in Anacharitinae, and the ovipositor as in Sarothrus opacus), we would probably obtain a "synethetic" insect bearing a greater resemblance in all the characters to the representatives of the three families of Diaprioidea mentioned earlier, than the resemblance observed between Diaprioidea and the "group Scelionidae". This does not mean, of course, that the boundary between Cynipoidea and Diaprioidea is poorly defined (the main distinguishing feature, i.e. the sensillae on the antennae, is found among Dioprioidea only in Mymaridae, which differ markedly from Cynipoidea in the other characteristics). However, the independent position of the two superfamilies should probably be substantiated further with additional evidence. p.96

The system of Cynipoidea is peculiar in the sense that their subfamilies are defined much more clearly than their families, the number and size of which are subject of considerable controversies. In this work we accept a system differing markedly from those used by most of the other authors (Hedicke, Kerrich, 1940; Muesebeck, Krombein, Townes, 1951; Weld, 1952; Riek, 1970b) with the exception of Richards (1956). It comprises only three families: Cynipidae, Figitidae and Ibaliidae. The latter family unites Ibaliidae and Liopteridae on the basis of a similar venation pattern (the primitive radial cellule without enlargement and the secondarily narrowed central cellule, the posterobasal corner of which is closer to R than to M+Cu), the proportions of the tergites (the sixth, less often the fourth or the fifth tergite is the largest one or at least is longer than the third tergite), a similar structure of the hind legs (that

are markedly enlarged, particularly the coxae and the first segment of the tarsus; the presence of a thick spine on the second segment of the tarsus in Ibalia and in some Liopterinae and Mesocynipinae), and parasitism of xylophages. Hedicke and Kerrich (1940) list the following characters of Liopteridae in addition to the proportions of their tergites: the joint of the propodeum raised above the coxae and the presence of a longitudinal keel on the lower surface of the propodeum (underneath the articulation opening). The keel is also characreristic of Ibalia and Anacharis; in some Mesocynipinae (particularly in Kiefferiella Ashm.) the articulation aperture is not raised above the coxae, but is displaced backwards (the lower surface of the propodeum is elongated, as in the other Liopteridae, but is disposed horizontally instead of being slanted upwards); the same is characteristic of Ibalia and of a number of other Cynipoidea. Ibalia differs from Liopteridae in having a long abdomen flattened in a cultiform manner, a very narrow radial cellule, in having an areola and a particularly strongly elongated first segment of the posterior tarsus; these characters appear to be as substantial as those differentiating Liopterina, Oberthuerellinae and Mesocynipinae, which formerly constituted the family Liopteridae.

Apart from Figitinae, Aspiceratinae and Anacharitinae that are always included into Figitidae, we have also referred to this family Eucoilinae, Pycnostigmatinae and Charipinae that are usually assigned to Cynipidae because of their markedly enlarged second tergite. Since the "second" tergite of Eucoilinae and Pycnostigmatinae is composed in reality of the fused second and third segments in males and second-fourth segments in females, and since their actual proportions are unknown, this characteristic loses its significance in our case. Eucoilinae and Pycnostigmatinae are similar to Figitidae with regard to the venation (the central cellule extends completely to Cu, whereas in Cynipinae it normally ends far short of it, but, in contrast to Ibaliidae, closer than to R); their characteristically enlarged and folded under seventh tergite and the lack of the median suture on their mesonotum, while the notaulae are present, are also features more typical of

Figitidae than of Cynipinae, even though they may be found in the latter. An additional (though not very reliable, like all the symplesiomorphisms) indication that Eucoilinae are close to Figitinae and Aspiceratinae is the retention by these insects of their initial assortment of hosts (dipterous insects; the biology of Pycnostigmatinae is unknown). All these factors compel us to include the two families discussed into Figitidae.

Charipinae are similar to Cynipinae in the shape of their central cellule ending normally far short of Cu, and because of their large second tergite of the metasoma. The former attribute is advanced and apomorphous, but it would be risky to qualify it as a character inherited from a common ancestor, since both groups include forms with the cellule, the posterior margin of which is proximally curved backwards and oriented towards Cu (among Cynipinae this has been observed, for example, in the Aulacidea salviae Först., and among Charipinae - in species of the genus Alloxysta Först.). As concerns the metasoma, in addition to the second tergite, the third tergite of Charipinae is also markedly enlarged and may even be distinctly longer than the preceding one (in Alloxysta, the form mentioned earlier). The second tergite of Cynipinae may be shorter than the third one (for example, in Ceroptres Hartig), but Charipinae are nevertheless as close to Figitinae as to Cynipinae with regard to the structure of their metasoma. Keeping in mind that parasitic Charipinae could not have descended from the secondarily phytophagous Cynipinae, and that some Charipinae are similar in the structure of the abdomen (Dilyta Först.) and in other characters (see Riek, 1970b) to Eucoilinae, it is more logical to treat Charipinae as forms close to the other parasitic Cynipoidea and as members p.97 of the family Figitidae, and to restrict Cynipidae to the status of a nominal subfamily.

Most of the families and subfamilies of Cynipoidea are widely distributed in the recent fauna; relatively narrow ranges are characteristic only of the subfamilies of Ibaliidae (Ibaliinae in the Holarctic regions, Liopterinae in the Neotropical

realm, Oberthuerellinae in the Ethiopian realm, Mesocynipinae mainly in the Australian and Oriental realms, but penetrating also into the Nearctic and Eastern Palearctic realms, including our Far East; Belizin, 1961). In addition to this we should stress the remarkable paucity of the Cynipoidea fauna in Australia, in particular the absence of non-imported gall-forming forms, instead of which we find there gall-forming Chalcidae (Riek, 1970b).

The oldest known Cynipoidea have been derived from the Taimyr and Canadian resins dating back to the latter half of the Cretaceous (the Santonian from Yantardakh and the Campanian from Cedar Lake), where there have been found Cynipidae of the most primitive tribe Aulaxini (representatives of which also predominate among the Cenozoic fossil Cynipoidea); in Yantardakh we also found Ibaliidae Mesocynipinae. The earliest Figitinae have been found in Baltic amber of the Eocene age and in amber from the Sakhalin peninsula, the age of which within the Paleogene has not been determined. The other subfamilies have not been identified with confidence in fossil state*, which is particularly surprising in the case of the subfamily Eucoilinae that can be diagnosed relatively easily.

All the three families of Cynipoidea have both primitive and advanced characteristics and none of them can be derived from either of the others. If we take the conjunction of their characteristics, Figitidae appear to be the least modified family of the three. Admittedly, they appear later than the two other families, but this may be due not to their late appearance as such, but to the late flourish of their principal hosts, i.e. of the higher Diptera, and the resulting scantity of all the parasites of these insects prior to the Neogene.

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* The Protoibalia Brues from the Oligocene of the USA (Florissant) that as been described as a representative of Ibaliinae (Brues., 1910), may belong in reality to Mesocynipinae.

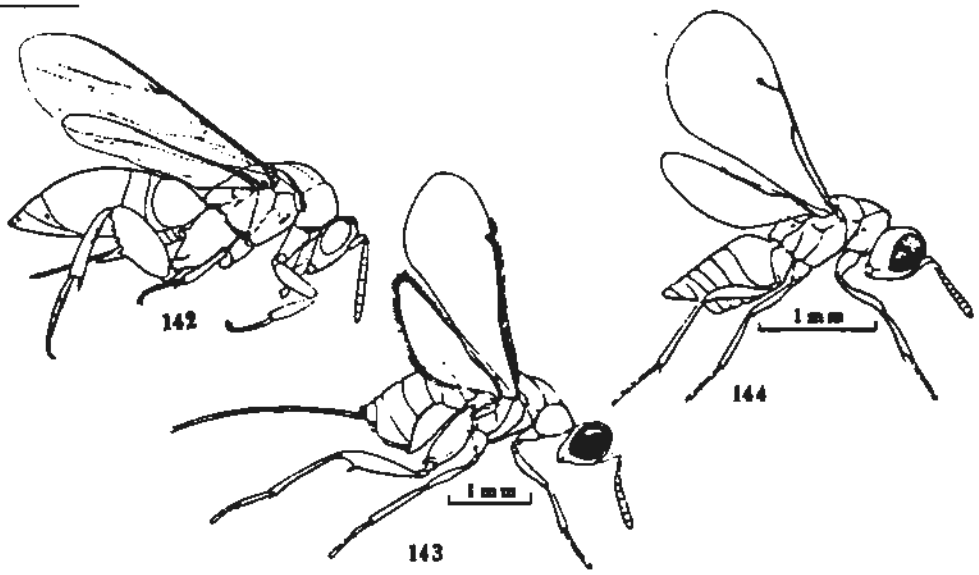
Chalcidoidea

The superfamily Chalcidoidea (figs 142-144) forms one of the largest and well segregated groups of Hymenoptera. They are characterized by the following combination of characters. Antennae with 13 or fewer segments, a long scapus, and almost always with a few ringlets (minute segments) posteriorly of the pedicle; segments commonly with sensillae (neither the ringlets, nor the sensory crests are developed, for example, in Leucospidinae); well-defined sexual dimorphiss of the antennae. The head is closed by the lower tentorial bridge or (commonly in the smallest forms) by closed hypostomes. Prothorax with abbreviated posterior corners ending short of the tegulae (if the latter do not form a slender projection oriented forwards, as in Leucospis F.). Postspiracular sclerites nearly always free (very rarely fused with the posterior corners of the pronotum, as in Stilbula Spin., but not with the mesopleura); outer sclerites (hidden underneath the pronotum in Chalcis F.) are separated from one another or merging into a half-ring. Propodeal aperture without the tooth-shaped condyles. Wings with a distinctive markedly reduced venation; pterostigma lacking; the only apically ramified vein of the anterior wing is formed by R and by 2r-rs diverging off R; this vein may also be abbreviated. In many instances 2r-rs terminates apically in two distally oriented processes which may continue on secondarily enlarged forms in diffuse vestiges of veins; taken in conjunction with the traces of the other veins, they produce a pattern very similar to the venation of Pelecinus. Apart from R bearing apically 2-3, rarely as many as 6 closely spaced hooklets, we may find in the posterior wing r-m (commonly in the form of a trace) resembling in shape the corresponding vein of Mesoserphidae and Dioprioidea (relatively short and C-shaped) or (as in Leucospis) that of Proctotrupidae and Heloridae (long, S-shaped, and nearly parallel to the anterior edge of the wing). The first segment of the metasoma is annular or tubular, commonly without a distinct boundary between the tergite and sternite (the tergite and sternite are not fused, for example, in Leucospis, but this may be a secondary effect of the reduction of that segment, which

p.98

in this form, as well as in a number of other Chalcidae, is quite considerable). The length and shape of the succeeding tergites and sternites are highly diverse; the apical sclerites are not tightly in contact, the ovipositor is of the external type or retracted into the metasoma. Male genitals without the basal ring. Development ecto- or endoparasitic; assortment of hosts very large: many forms are egg parasites, but there are also phytophagous forms among them (parasites of seeds or gall-forming insects). A number of chalcids, including extoparasitic forms, develop in the larvae of xylophagous insects. Pupation almost invariably without the cocoon and wherever a cocoon is used, it is made out of the matter secreted through the anal opening.

Figs. 142-144



Representatives of the superfamily Chalcidoidea (all recent). 142-Polistomorpha surinamensis Westw., Leucospidinae; 143-Diomorus sp., Torymidae; 144-Nasonia vitripennis Walk., Pteromalidae (142-from Boucek, 1974; 143-144---from Riek, 1970b).

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Among the characters listed above the most important diagnostic features are as follows: the presence of ringlets numbering more than one among the other Ichneumonomorpha (one single ringlet has been recorded for example, in Ichneumonidae, Heloridae and Diapriidae Ambositrinae; more than one ringlet is known only for Chalcidae), the presence of the outer post-spiracular sclerites (with rare exceptions), the character of venation (a similar venation pattern has also been encountered in Scelionidae), and the absence of the basal ring in the genitals (which is also characteristic of Mymaridae).

The most important features for determining the relationship of Chalcidae with the other Microhymenoptera are their venation (rudiments of the veins branching off 2r-rs and the shape of r-m in the posterior wing), the long scape and sex dimorphism of their antennae, their free postspiracular sclerites and their ectoparasitism (particularly the existence of exto-parasites of xylophages). The latter characteristic denotes the direct relationship of these insects with Mesoserphidae, whereas the structure of their antennae resembles more closely that of Diaprioidea. The venation of the anterior wing and some variants of venation of the posterior wing (in Leucospis) account for the resemblance of Chalcidae to Proctotrupoidea, but the predominance of the venation pattern of the posterior wing that is more typical of Mesoserphidae and Diaprioidea, evidences that it is a common tendency rather than an inherited resemblance. The free post-spiracular sclerite has been recorded not only in the chalcids, but also in the primitive Diaprioidea, which may have inherited it from Mesoserphidae. The structure of the antenna, as well as the shape of the pronotum in Austroniidae and Monomachidae resembles that of Chalcidae and brings the latter closer to Diaprioidea. p.99

The characters listed above thus suggest contradictory conclusions regarding the phylogenetic relationships of Chalcidae: some of these characters point to their relationship with Mesoserphidae, others with Diaprioidea. The latter variant is rather implausible. Chalcidoidea could have originated from Diaprioidea only if the primitive representatives of the latter

were still ectoparasitic or if the reversal of endo- to ectoparasitism were possible. In the contrary event we are obliged to derive the chalcids directly from Mesoserphidae. The relatively late (in the middle of the Cretaceous) appearance of the chalcids in the fossil record appears to testify in favour of their having originated from Diaprioidea. But the absence of older chalcids therein may be due to these minute insects being usually found in the fossil record in the form of inclusions in resins which have not been found in the Early Cretaceous and, particularly, Jurassic deposits or (Lebanese) have been inadequately studied.

The lack of data pertaining to the group discussed compels us to abandon any attempt at analyzing the system and phylogenetic relations within the superfamily Chalcidoidea. The same paucity of information and the extremely inadequate extent to which the Tertiary chalcids have been studied make it impossible to analyze in detail the paleontological history of the superfamily itself. We can only state on the basis of the work by Yoshimoto (1975) and of V.A. Tryapitsyn's data on the chalcids from Taimyr resins (personal communication) that Tetracampidae Baemorphidae and Ormyridae constantly predominate among them. Furthermore archaic Torymidae and Ormyridae are present in the Santonian of Taimyr (Yantardakh), while Tetracampidae Bouceklytinae and Trichogrammatidae are found in the Campanian of Canada (Cedar Lake). At the beginning of the Late Cretaceous (Late Cenomanian in Taimyr, Agapa) the finds of Chalcidoidea are still very rare, but subsequently they become more and more common. From the Cenozoic there have been reported predominantly Torymidae (predominating absolutely in the Baltic amber of the Eocene age; identification by V.A. Tryapitsyn) and Chalcididae. Furthermore, there have been recorded finds of Agaonidae, Cleonymidae, Eupelmidae, Eurytomidae, Perilampidae and Pteromalidae (Yoshimoto, 1975).

Chapter 4

The evolution of Vespomorpha

The early stages of the evolution

As was mentioned earlier, the evolution of Vespomorpha involved mainly modifications of the preying behaviour of the females: the search for the prey in the substratum (probably of beetle larvae in decayed wood) and their infestation by a direct contact* instead of by injuring the victim through the substratum with the ovipositor, as was the case with their ancestors Ephialtitidae. All this was accompanied initially by relatively minor morphological changes: the acquisition of the characteristic vespine habit, the drastic reduction of the outer parts of the ovipositor, perhaps also by the oligomerization of the segments of the antennae. The ideal structure of the abdominal articulation characteristic of Vespomorpha may have been derived from the common ancestor of Vespomorpha and Ichneumonomorpha. As concerns the antennae, polymerous antennae are known only in two families of the infraorder: in Sclerogibbidae and in two genera of Bethylonymidae (Arthrogaster A.Rasn. and Leptogastrella A.Rasn.). These two genera, the former one in particular, have fairly little in common with the other Bethylonymidae and it may easily turn out that they don't belong to Vespomorpha at all. Sclerogibbidae are among the most markedly aberrant Vespomorpha and their multi-segmented antennae may be simply yet another of the many unusual specializations of these insects.

The primitive Vespomorpha were probably Bethylonymidae (figs. 145-146) forming a separate superfamily Bethylonymidae.

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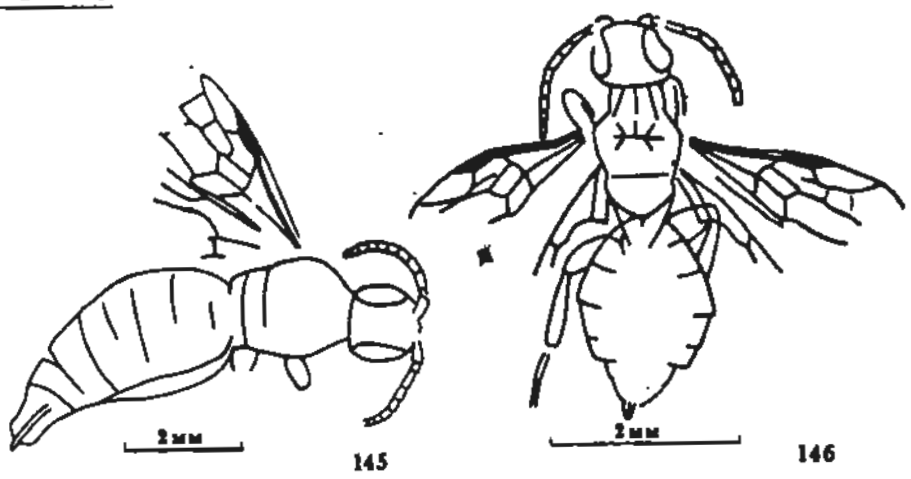
* The hypothesis that primitive aculeate insects or their ancestors preyed on insects living in the open (Tobias, 1975a; Brothers, 1975), does not apply to Jurassic Bethylonymidae. These insects are very similar in appearance to Bethylidae and Tiphiidae, and it is rather improbable that they would have preyed in the open rather than within the substratum.

Figs. 145-146



Representatives of the family Bethylonymidae (Upper Jurassic, Southern Kazakhstan; from Rasnitsyn, 1975a).
145-Bethylonymus curtipes A.Rasn.; 146-Bethylonymellus cervicalis A.Rasn.

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Most of the known forms have been found in the Late Jurassic of Karatau; one of the remains comes from the Middle or Upper Jurassic deposits of the trans-Baykal region (Uda). Bethylonymidae resemble in appearance Bethylidae and have a primarily complete venation with no distinctive characteristics, and a short (commonly very short, but external) case of the ovipositor. The latter character suggests that the internal ovipositor of Vespomorpha developed initially by way of the reduction of its outer parts rather than through its retraction inside the metasoma, and that the modification of the inner parts of the ovipositor distinguishing Aculeata (i.e. Vespomorpha without Bethylonymidea) from the other Hymenoptera occurred at later stages in the evolution of that infraorder, i.e. at the time when Aculeata arose. The structure of the ovipositor in Bethylonymidea may have been essentially the same as in the other higher Hymenoptera.

Aculeata evolved from Bethylonymidea roughly at the Jurassic-Cretaceous boundary; their first (but not the most primitive) representatives are already known from the Neocomian.

The evolution of Aculeata was accompanied mainly by modifications in the structure of their ovipositor that may have been associated with improvement of its invagination into the metasoma, may have been aimed at providing for more accurate and freer movements of the ovipositor while it injures the prey, or, may have been related to the loss of the primary function of the ovipositor, i.e. the passage of the egg. At least it is believed that the ovipositor of Aculeata is free of that function, even though not all the forms that are of interest in this respect have been studied as yet and there are indications that in some Bethyloidea the ovipositor is used for passing eggs as well as toxin (Oeser, 1961 as quoted in Imms, 1957). It is, indeed, rather improbable that Embolemidae and Dryinidae, which embed their eggs completely or to a large extent into the body of their host (Bridwell, 1958; Ponomarenko, 1975a), could lay eggs without passing them through the canal of their ovipositor. Sapygidae may not be able to do so either (Lith, 1957).

The distinctive characters of the ovipositor and of the adjoining sclerites of the metasoma in Aculeata (fig. 147) are as follows [we use here many of Oeser's date and conclusions (Oeser, 1961)]:

1. A deep notch on the ventral margin of the second valvifer extending as far as its thickened dorsal margin and beginning more distally than the joint of the second valves of the ovipositor with the valvifer; as a result of this the latter is differentiated into the distal and proximal sclerites with the former bearing the protective case (the third valves of the ovipositor), while the latter is primarily articulated with the bases of the second valves (this joint may be secondarily lost, then be restored once again with the process of the distal sclerite, as is the case, for example, in Bethylidae). p.101

2. The presence of the one single stemming plate on the inner dorsal costa in each valve of the first pair; moreover, that plate is composed of one or two thin fragments of the membrane raised above the valve on the median process (an outgrowth of the dorsal margin of the valve), and is disposed at the same

level as the basal part of the fused second valves. Oeser (l.c.) believes that the stemming plates appeared repeatedly, a number of times, but it is difficult to agree with this view, at least with reference to Aculeata. As is known, these plates are lacking in Plumariidae, Pampilidae, Sapygidae s.l. (including Fedtschenkiidae), Tiphiidae and Thynninae, in some Bradynobaenidae (in Bradynobaeninae and Typhoctinae, but not in Apterogyninae or Chyphotinae), in Vespoidea and in some ants, i.e. mainly in representatives of Aculeata s.str. (the Aculeata without Chysidoidea=Bethyloidea; the priority of the former name was demonstrated by Day, 1977). In this group the structure of the stemming plates, when they are present, is so standard and characteristic (two lamellas per median process) that we cannot accept the hypothesis of their multiple reappearance.

3. The case of the ovipositor is often and, probably, primarily divided into two segments.

4. The eighth tergite in females is without the basal apophyses.

5. The cerci are reduced in females.

The problem of the furcula, an additional sclerite at the base of the second valves, is more complex. A typical furcula joined to the base of the second valves with the tips of its branches is, indeed, characteristic only of Aculeata, but is lacking in some of them or has a different structure. The furcula is absent in some representatives of Chrysidoidea (Sclerogibbidae, Dryinidae and Embolemidae) and in ants; some of the forms lack not only the branches, but even the enlargement at the point of the junction with the valves (in Chrysididae, where, in addition to it, the opposite end of the furcula is split); in Scolebythidae the branches are present, but do not participate in the articulation. The presence in some Ichneumonoidea and Evanoidea (see Oeser, 1961) of a structurally simple sclerite which has, however, a similar position to that of the furcula, suggests that the furcula may have appeared independently, and its absence in some of the ants indicates that it may have been reduced. The problem

of whether the absence of the furcula in the three families of Chrysidoidea listed above is primary or secondary should therefore be left open, and in characterizing Aculeata it may be more accurate to state that they exhibit a strong tendency to develop a furcula rather than to say that it appeared in their common ancestor.

Aculeata.

The system and phylogenesis of Aculeata were recently analyzed in detail by Brothers (1975). The conclusion drawn by that author regarding the phylogeny of Aculeata and our own data obtained for the most part independently of Brothers from the research performed for this work, disagree only in a few points. This pertains first of all to the relationships between Scoliidae, Sapygidae and the group Pompilidae+Rhopalosomatidae, and, to a lesser degree, to the relationship of Scolebythidae, Plumariidae and the other Chrysidoidea, the links between which Brothers does not analyze. Our disagreements are partly due to the fact that Brothers was not familiar with descriptions of many extinct (Baissodidae and other Early Cretaceous wasps) and some recent Aculeata (Proscolia A.Rasn., Scoliidae) that are vital for understanding the problem examined, and partly because of the differences in our respective assessments of the plesiomorphous and apomorphous states of some of the characters.

The system accepted for Aculeata in this work is of a more traditional nature with regard to the superfamilies than that adopted by Brothers. Brothers includes Pompiloidea, Scolioidea and Formicoidea into Vespoidea believing that they all diverged as one single stem off their common ancestor with Sphecoidea (which is dubious in the case of Pompiloidea) and that the differences within Vespoidea are too minor to divide this group into superfamilies. Here our disagreement is of a more subjective nature, even though the system proposed by Brothers is based on the mathematical evaluation of the differences between the groups. The reason for this is that, when used in systematics, the

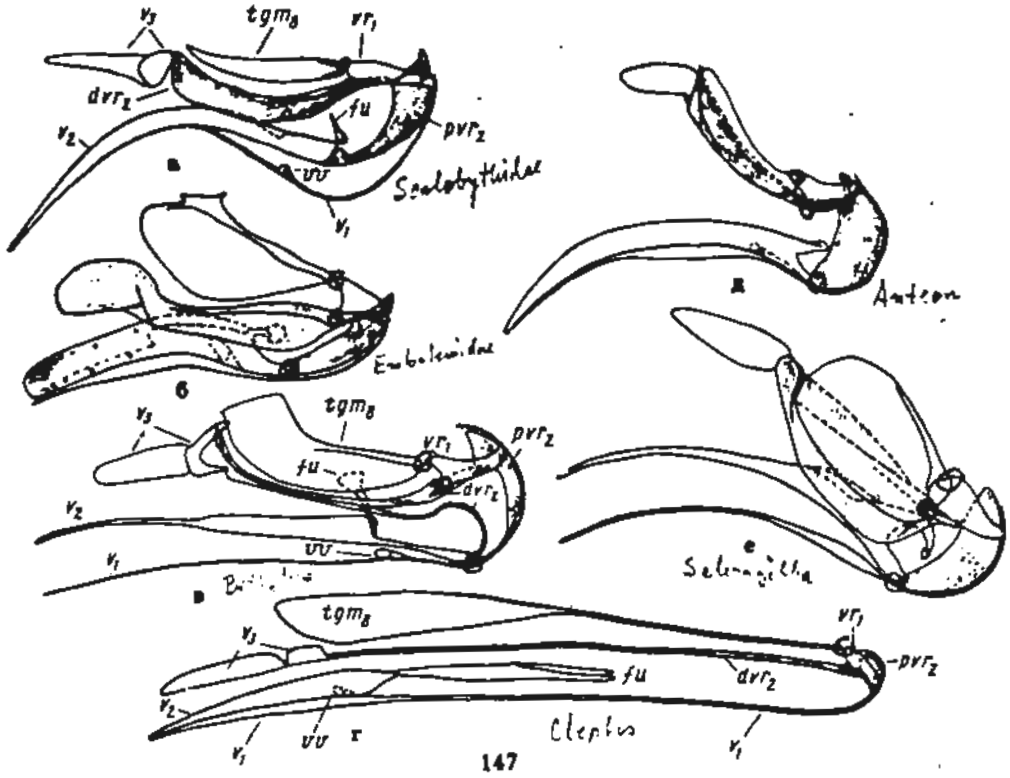
p.102

objectivity of mathematical methods is highly relative, since the results of their application depend to a great degree on the choice of the method of assessment, which is a fairly subjective factor (Ponomarenko, Rasnitsyn, 1971; Rasnitsyn, 1972b). The difference between the system of the bees and fossores (Sphecidae) worked out by Brothers and that adopted by us in this work is even more subjective (in Brothers's interpretation these are two "informal groups of families", in our system - two families within a superfamily). We feel that the coincidence of the results (recognition of the bees and fossorial wasps as equivalent groups with an analogous structure and as members of the same superfamily) is considerably more important than the differences in the evaluation of the ranks of the subordinate taxa. Brothers "equalizes" the fossores with the bees by dividing them into families and by setting apart the informal groups Apiformes and Spheciformes. In our opinion the opposite solution would be more justifiable, i.e. amalgamation of all the bees within one single family, as is done for the fossorial wasps. Michener (1974, pp. 3 and 21), the greatest specialist on bees, is also inclined to accept this viewpoint.

Having said this, we shall refrain in further account from mentioning all the instances of coincidences and disagreements of our views with those of Brothers, but shall reserve our discussion for the most important cases of the non-coincidence of our results.

The first divergence recorded for Aculeata occurred p.104
not later than at the very beginning of the Cretaceous period and led to the appearance of Chrysidoidea on the one hand and of the ancestor of all the aculeate insects on the other. The latter can be referred to after Oeser (1961) as the Aculeata proper (Aculeata s.str.). The time of the divergence is determined by the presence of the representatives of both groups in the Neocomian (the beginning of the Early Cretaceous).

Fig. 147



Ovipositor of Aculeata (schematic).

a-Clistopsenella longiventris Kieff., Scolebythidae; b-Embolemus ruddii Westw., Embolemidae; c-Bethylus sp., Bethylidae; d-Cleptes sp., Chrysididae; e-Anteon brevicorne (Dalm.), Dryinidae; f-Sclerogibba sp., Sclerogibbidae; g-Bembix rostrata L., Sphecidae; h-Fedtschenkia anthracina Ashm., Sapygidae: i-Methocha ichneumonoides Latr., Tiphiidae; j-Myrmosa brunnipes Lep., Mutillidae; k-Apterogyne mlokosiewitzi Rad.; l-Chyphotes petiolata Fox.; m-Typhoctes peculiaris Cress.; n-Bradynobaenus gayi Spin. (k-n are Bradinobaenidae); o-Sierolomorpha canadensis Prov., Sierolomorphiade; p-Myrmecia vindex F.Smith, Formicidae; r-Eciton burchellii Westw., Myrmicidae (all recent; g-from Oeser, 1961; p-after Hermann, 1975, simplified; the others are original drawings).

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Fig.. 147 Continued

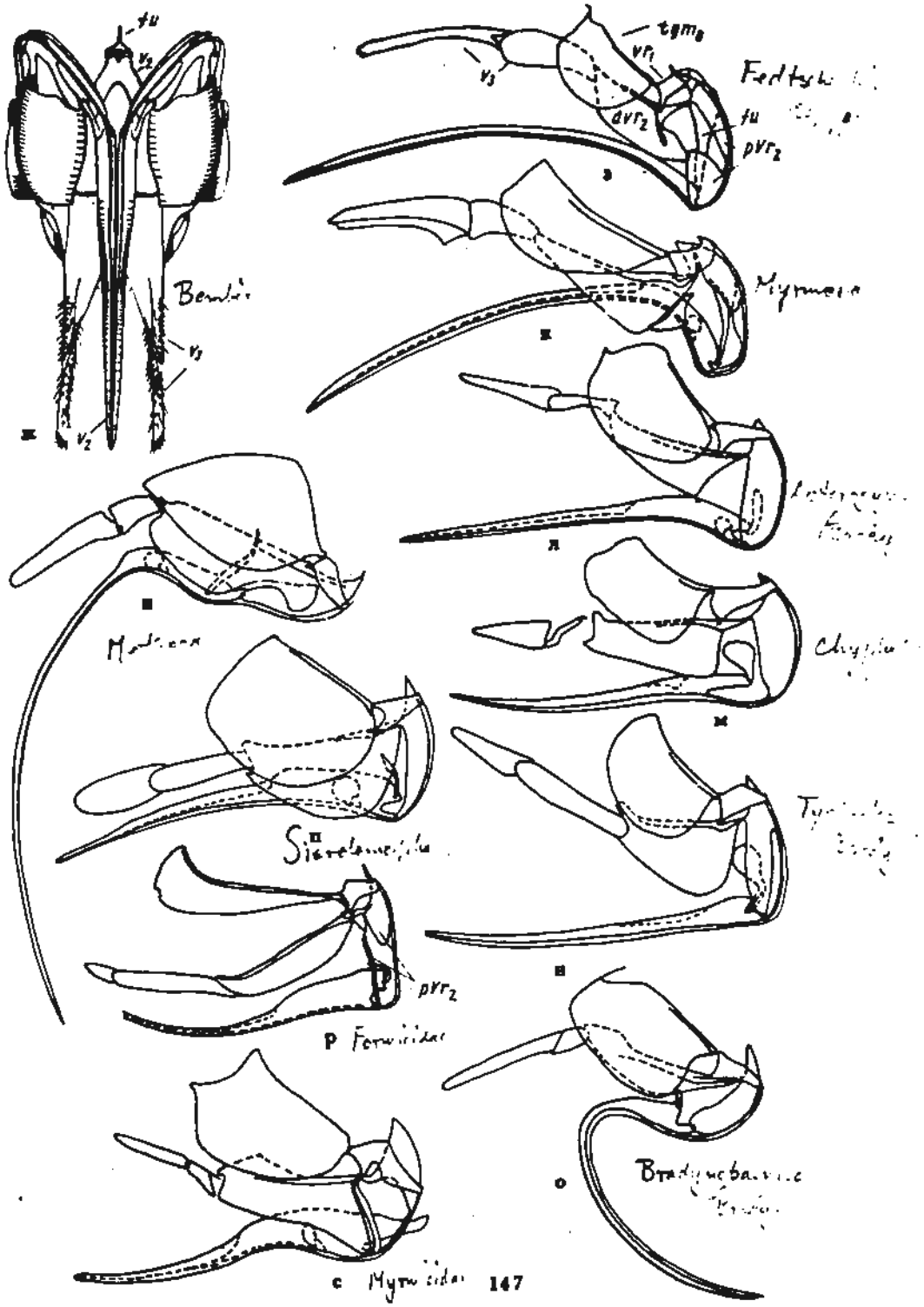


Рис. 147 (окончание)

The appearance of Chrysidoidea was accompanied, according to Brothers, by the development of a joint inside the second valvifer of the ovipositor (in Brothers - the goncoxite IX ♀) and by reduction of the jugal lobe in the hind wing. The latter character may, however, be pleiomorphous, since Karatavitidae are so far the only Jurassic forms of Apocrita in which the jugal lobe has been found, and we have no grounds to assume its presence in the ancestor of Aculeata. It is more probable that the jugal lobe (which is weakly separated from the anal lobe even in Karatavitidae) lost its discrete position in Ephialtitidae. This condition persists in most of the numerous descendants of Ephialtitidae, and the anal lobe divides once again into two (the anal lobe itself and an analogue, though not necessarily a complete homologue, of the jugal lobe found in the lower Hymenoptera) only in Aculeata s.str. and, independently of them, in Evaniidae.

On the other hand there are additional autapomorphisms in Chrysidoidea, which Brothers failed to mention: the slender straight anterior pedicles of the tentorium (in Embolemidae they are secondarily complicated by lamellar processes), the furcula of the prothorax jutting forward (it is markedly modified secondarily in Sclerogibbidae), and the reduction of the venation (at least the absence of 2m-cu or its presence in the form of a weak trace) that may be related to the decrease in the body measurements characteristic of Chrysidoidea.

The modifications which led to the appearance of Aculeata s.str. were different. Brothers refers to their autapomorphisms the stabilization of dimorphism in the composition of their antennae (12-segmented antennae in females, 13-segmented in males) and the hidden centrally membranized metasomal tergite of the female. The two-lamellar stemming plates of the first valves of the ovipositor and the jugal lobe of the posterior wing should probably also be referred here. The modified shape of the mandibulae with the sectorial edge turned over so that it is parallel to the place in which the mandible moves, may prove to be primary for Aculeata s.str. The mandibles of Vespidae Polistinae

are more primitive and are similar to those of many Bethyloides and more primitive Hymenoptera (with four denticles that are perpendicular rather than parallel to the plane in which the mandible moved), but so far it is not clear whether their shape is an inherited or a secondary character.

Chrysidoidea

The size and composition of the superfamily Chrysidoidea (=Bethyloidea) (figs 148-158) are here the same as in Brother's works, but its organization is somewhat different from the generally accepted scheme. The size of the families Bethylidae, Dryinidae, Embolemidae, Sclerogibbidae and Scolebythidae remains unchanged. We included, after Brothers, the nominal subfamily of the family Heterogynidae instituted by Nagy (1969, 1970) into Plumariidae; according to Brothers, the second subfamily Ticoplinae belongs to Mutillidae. We referred to Chrysididae not only Cleptinae, Amiseginae and Adelphinae (Muesebeck, Krombein, Townes, 1951), but also Loboscelidiinae (Krombein, 1957). The close relationship of the latter to Amiseginae and Adelphinae is corroborated first of all by the extremely close resemblance of the structure of the genitals and of the last abdominal segments in their males (the structure of the ovipositor and the apex of the abdomen in females have not been described) and, secondly, by their distinctive biology, i.e. parasitism of eggs of Phasmides (stick insects) (Krombein, 1957, 1960; Riek, 1970b). The unity of all the Chrysididae manifests itself in the distinctive structure of the last abdominal segment in females where it is modified to a telescopic (retractable) ovipositor, and in the similar structure of their ovipositor as such (these organs have not been described for Loboscelidiinae, but their similarity in other respects suggests that the above statement is equally valid for them). A certain p.105
similarity has also been recorded in the biology of Chrysididae: primarily these insects (i.e. Cleptinae and many Chrysidinae) parasitize the larvae of Hymenoptera and Lepidoptera enclosed in cocoons or cells; moreover, in doing so, they gnaw rather than

pierce through the cocoon with their ovipositor (Clausen, 1962). The other three families changed to developing in superficially similar objects, such as eggs of stock insects (the morphotypical evolution of parasitism, according to Kozlov, 1970), but retained their original mode of oviposition through the openings made by gnawing (Krombein, 1960).

Chrysididae resemble most closely Bethylidae. This is evident first of all from the existence of a group intermediate between them (bethylids of the subfamily Mesitiinae). Moreover, the Eocene form Uromesitius Brues practically bridges the gap between the two families (Brues, 1933a). It is interesting to note that Mesitiinae attack at least occasionally the larvae of the leaf parasites Clytrinae living inside protective cases (Mocsar, 1971). This may also be regarded as a character in which Mesitiinae are close to Chrysididae, for which parasitism of insects existing in cocoons is probably primary. Furthermore, both families lack the joint of the second valves of the ovipositor with the proximal part of the second valvifer (in Bethylidae they articulate with the processes of the distal part of the valvifer, which appears to be a secondary character). Bethylidae and Chrysididae do, indeed, seem to be close. The question of whether the latter can be derived from Bethylidae, in particular from Mesitiinae, needs to be investigated further.

A number of characters relate the families discussed to Embolemidae. The latter are commonly believed to be close to Dryinidae on the basis of their 10-segmented antennae (in the other Bethyloidea the antennae have 13 segments; the only Plumariidae with 12-segmented antennae are Bethylidae Cephalonomiini and Myrmicopterinella Day, and the antennae of Sclerogibbidae comprise 17 to 40 segments) and their parasitism of Jugatae (Brothers, 1975). However, the antennae in these two families are similar only with regard to the number of their constituent segments, but differ markedly in structure. In Embolemidae the antennae are not geniculate in spite of their long scape, and the pedicle is connected to the flagellum in a fixed manner. In Dryinidae the scape is short, but the antennae are nevertheless

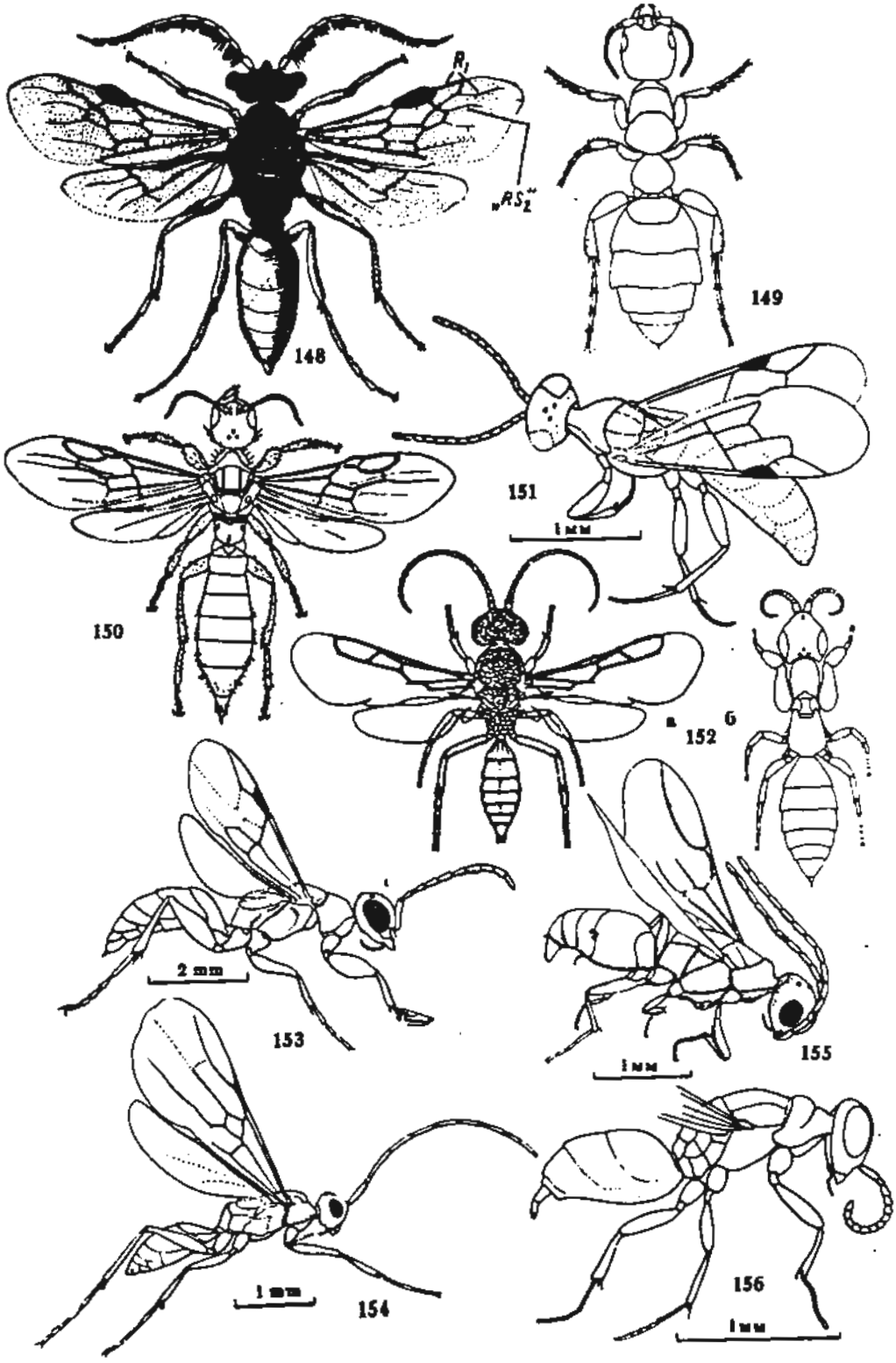
often geniculate in shape and the pedicle articulates in a mobile manner with the first segment of the flagellum. It is therefore doubtful that their resemblance has been inherited. Furthermore, Embolemidae do, indeed, develop on leaf-hoppers, similarly to Dryinidae (Bridwell, 1958), but their hosts (Achilidae) lead a confined mode of existence (developing in decayed wood) uncharacteristic of leaf-hoppers. Their similarity to Bethylidae and Chrysididae with regard to the habitat of their hosts (the topological specialization, according to the terminology of Kozlov, 1970) is, in our opinion, as important as the taxonomic closeness of the hosts of Embolemidae and Dryinidae. Furthermore, the completely endoparasitic development of Embolemidae finds its analogy among Aculeata only in Chrysididae, but not in Dryinidae which have a highly distinctive biology (N. Ponomarenko, 1975a). The only other character in which Embolemidae are similar to Dryinidae is the absence of the furcula at the base of the second valves in their ovipositor, but in the former family the stretched-out base of the valves is compressed into a vertical lamella resembling the unpaired part of the furcula in Bethylidae, and may be homologous with it.

We believe that the characters in which Embolemidae resemble Bethylidae and Chrysididae, are more substantial. Apart from the habitat of their hosts, it is first of all the structure of the two first sternites of their metasoma (fig. 159). The posterior edge of the first sternite is butt-joined to the second sternite; primarily it is more or less thick (secondarily the sternite terminates in Cleptinae and Chrysidinae in paired membranous lobules overlapping the base of the third sternite) and straight (in Chrysididae it is notched to varying degrees in the middle). In the other Bethyloidea the posterior margin of the first sternite is as thin as the margin of the other segments; it is broadly rounded and rests upon the second sternite (in Dryinidae Aphelopinae the posterior margin of that sternite is bi-lobed; this may be due to the fact that the sternites are laterally compressed and form a sharp virtually knife-like ridge along the median line, so that the resemblance of these forms to

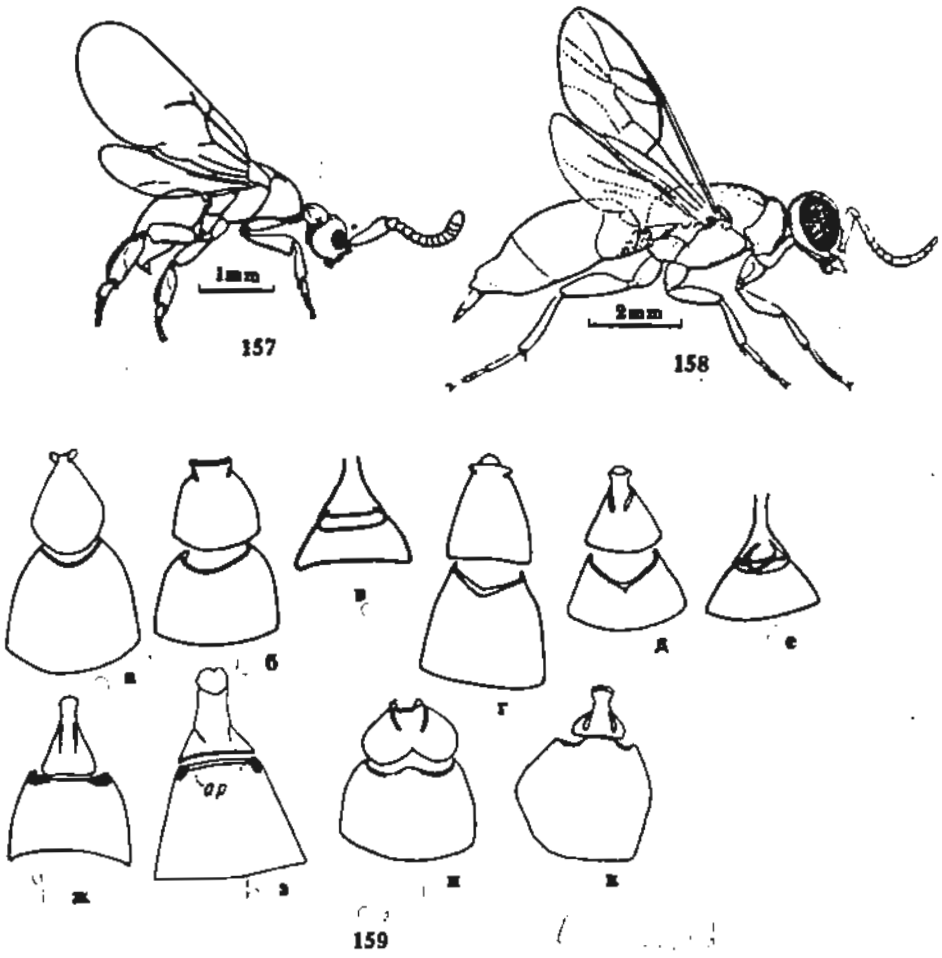
Chrysidinae and Cleptinae is rather superficial). In Bethylidae and Embolemidae the anterior margin of the second sternite is straight in its major part with small notches only near its lateral corners; the apophyses (bulges formed by the cuticle) are oriented upwards (inside the abdomen) and are disposed laterally next to these notches and away from the edge of the sternite; p.107
small desclerotized areas are situated posteriorly of the apophyses. In Chrysididae these areas expand markedly and may spread onto the anterior margin, which appears then to be deeply notched on the sides, and the apophyses become reduced (their rudiments are discernible in Adelphinae). In the other Chrysidoidea the anterior margin of the sternite is straight and deeply incurved (in Dryinidae and Sclerogibbidae it bears angular notches in the middle), without the invagination apophyses, but with the lateral corners stretched out forward.

Another character in which Bethylidae, Chrysididae and p.108
Embolemidae are similar, is the structure of their metathorax. In Bethylidae its middle portion is raised in the form of a clearly demarcated platform forcing the mesocoxae widely apart; it has a straight anterior margin and a bilobate (in Bethylinae) or pointed (in Epyrinae, Pristocerinae and Mesitiinae) posterior margin. In Embolemidae and Chrysididae it bears a median keel (in Cleptinae the keel is double), which may be the precursor or the rudiment of the broad platform. In the other Chrysidoidea (including, contrary to Brothers's view, Scolebythidae 1975) the metathorax is more or less flat (without the discrete platform or keel). According to Brothers, the platform is present only in females of Plumariidae and has then a different shape (unfortunately the author provided no detailed description or drawing of that element). Brothers believes the raised platform on the metathorax to be a primitive characteristic of all the Aculeata, but we find it difficult to agree with this view.

Figs. 148-156



Figs. 157-159



Figs. 148-158

Representatives of the family (sic) Chrysidoidea
148-Plumarius topali Nagy, ♂ ; recent; Plumariidae; 149-P. sp., ♀; recent; Plumariidae; 150-Ycaploca evansi Nagy, recent; Scolebythidae; 151-Cretabythus sibiricus Evans, Upper Cretaceous, Taimyr; Scolebythidae; 152-Probethylus schwarzi Ashm., recent: a-male, b-female; Sclerogibbidae; 153-Chelogynus sp., recent; Dryinidae; 154-Embolemus sp., recent; Embolemidae; 155-Holepyrus precursor Brues; Upper Eocene from the Baltic region; Bethylidae; 156-Hypocleptes rasnitsyni Evans; Upper Cretaceous from Taimyr; Chrysididae Cleptinae; 157-Loboscelidia sp., recent; Chrysididae

Loboscelidiinae; 158-Holochrysis sp.; recent; Chrysidinae (148-from Nagy, 1973; 149-from Evans, 1966; 150-from Nagy, 1975; 151, 156- from Evans, 1973; 152-from Shetlar, 1973; 153, 154, 157 and 158-from Riek, 1970b; 155-from Brues, 1933a).

Fig. 159
The first and second metasomal sternites of Chrysidoidea a-Plumarius sp., ♂, Plumariidae; b-Clistopsenella longiventris Kieff., ♀, Scolebythidae; c-Cretabythus sibiricus Evans, ♂; Scolebythidae (oblique posterior view; in reality the posterior margin of the sternites is rounded); d-Sclerogibba sp., ♀, Sclerogibbidae; e-Anteon brevicorne (Dalm.), ♀; Dryinidae; f-Pseudogonatopus distinctus Kieff., ♀; Dryinidae; g-Embolemus ruddii Westw., ♂; Embolemidae; h-Pristocera depressa (F.), ♂, Bethylidae; i-Cleptes semicyaneus Turn., ♂ ; Chrysididae Cleptinae; j-Loboscelidia rufa Fouts., ♂; Chrysididae Loboscelidiinae (c-Upper Cretaceous from Taimyr, holotype; all the other forms are recent; original drawings).

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This type of platform is, indeed, highly characteristic of the aculeate insects searching for prey inside the substratum (Bethylidae, Scoliidae and Tiphiidae; it is also developed in Bradynobaenidae, but their biology is not known), and may become reduced if the mode of preying alters, as is the case in Mutillidae (see below). It may turn out that the platform has also been reduced in Embolemidae and Chrysidae.

Since the search for prey in the substratum is presumed to be primary for all the Vespomorpha, it is logical to assume that the raised platform on the metathorax is also a primary character in these insects. The evidence available testifies, however, against that inference. In the Jurassic Bethylonimidae that platform probably was not developed as yet (the structure of the lower surface of their thorax is best observable in the holotype Bethylonymellus bethyloides A.Rasn.). The absence of the

raised platform in Sclerogibbidae and in ants, many of which are close in their mode of preying (inside the substratum) to the forms furnished with a platform of that kind, is highly significant. Sexual dimorphism in that character in Plumariidae, the females of which probably lead a fossorial existence (Evans, 1966), may also testify that the character in question developed independently (there appear to be no other known cases of such a marked dimorphism in the structure of the metathorax).

Given the above considerations, it would be more rational to talk of the synapomorphism of Bethylidae, Chrysididae and Embolemidae with respect to the structure of their metathorax than of their symplesiomorphism.

Among the remaining four families of Bethyloidea certain links based on presumed synapomorphisms may be inferred between Dryinidae and Sclerogibbidae. The two groups are specialized along different lines and are totally dissimilar in appearance. It suffices to mention the multi-segmented (apparently secondarily) antennae attached underneath the projection of the frons in Sclerogibbidae, and their very short limbs on the one hand, and the normally disposed 10-segmented antennae and normal, often rather long limbs of Dryinidae on the other. Some of their features of similarity are, however, fairly significant: the second sternite of their metasoma bearing an angular notch in the middle and having an expanded acrosternite, the stretched-out base of the second valves of their ovipositor (even though the process thus formed differs in shape in the two groups), the enlarged ungues of the anterior tarsi in their females (only one unguis is enlarged in Dryinidae and only in some of them, so that this is a common tendency rather than a common character), and, lastly, their ectoparasitism of active hosts which, moreover, do not belong to insects with complete metamorphosis, as is the case with the other Chrysidoidea (excepting Embolemidae and Chrysididae).

The two remaining families Scolebythitidae and Plumariidae appear to have been the earliest groups to diverge off the common stem of Chrysidoidea. The characters testifying to that

effect are the primitive structure of their basal metasomal sternites, ovipositor (in Scolebythitidae; the ovipositor of Plumariidae has not been described in detail as yet) and metathorax (except in females of Plumariidae), and the complete venation of their wings, particularly of the posterior wings (in Plumariidae; the venation of their anterior wings is also very profuse, but it is complicated by the Z-shaped flexure of R and by the presence of the secondary "RS_2"). Day (1977) points out the similarity between Plumariidae and Scolebythidae, while Brothers believes on the contrary that Plumariidae branched off the stem of Chrysidoidea (referred to in Brothers's work as Bethyloidea) considerably earlier than Scolebythidae. In his analysis Brothers fails, however, to take into account the most primitive representatives of Scolebythidae (Cretabythus Evans and Ycaploca Nagy; Evans, 1973; Nagy, 1975), and examines chrysidoids that do not belong to the two families mentioned above, together as the "Bethylid group". In fact the only feature supporting that viewpoint is the reduced venation of Scolebythidae (particularly in their posterior wing) that is similar to the venation of more advanced Chrysidoidea, but is not a particularly reliable criterion. Admittedly, the nearly complete reduction of the venation in the hind wing combined with a very moderate (primarily) reduction of the veins in the anterior wing is characteristic of most chrysidoids (except Plumariidae), but is highly unusual in the aculeate insects, even though it has been encountered occasionally in other groups (Nitela Latr., Sphecidae). This character alone is not, however, a sufficient criterion for stating with confidence that Scolebythidae are close to the advanced Chrysidoidea. As concerns the reduction of the medial segment of the boundary between the metapostnotum and the propodeum, which, according to Brothers, should be regarded as a synapomorphism of Scolebythidae with his "bethylid group", in reality that boundary is also complete in Scolebythidae (fig. 150); moreover, the postnotum is expanded centrally backwards. This may be a primitive condition, since it has been observed, for example, in Stephanidae and Trigonalidae and is also

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characteristic of Ceropales Latr. among Pompilidae, as well as (though in a hypertrophied state) of Sphecoidea. The posterior boundary of the metapostnotum also persists in primitive Dryinidae (Aphelopinae and Anteoninae).

Scolebythidae, particularly the recently described (Evans, 1973; Nagy, 1975) Cretabythus Evans and Ycaploca Nagy that have not been taken into account by Brothers, display many primitive characters which Plumariidae and many of the higher Chrysidoidea no longer have. These characters are as follows: the minimal sex dimorphism; the primitive (relative to the other Scolebythidae) structure of the prosternum and anterior coxae (established only in Cretabythus); the moderately well-proportioned limbs; the metathorax without the keel or raised platform; the structure of the metapostnotum described earlier; the relatively small (in Cretabythus) first sternite of the metasoma with a thin rounded posterior margin. The structure of their ovipositor is primitive compared to that of the advanced Chrysidoidea (fig. 147, the ovipositor of Plumariidae has not been described in detail; Brothers indicates one single character that may be apomorphous, i.e. the absence of the stemming plates on the first valves). The known features of biology of Scolebythidae (which parasitize wood-gnawing insects, Cerambycidae in particular; Nagy, 1975) and Plumariidae (which probably attack insects living in the soil; Evans, 1966) are equally close to the presumed biology of the ancestors of Aculeata (preying on the larvae of insects, probably, beetles, living in the ground-cover or, more probably, in decaying wood). It would therefore be wiser to abstain for the time being from drawing definite conclusions as to which one of the two families discussed diverged earlier off the main stem of Chrysidoidea.

The paleontological history of Chrysidoidea begins in the early Cretaceous period. The fairly highly specialized family Dryinidae unexpectedly proved to be the oldest one. New collections from Bon-Tsagan in Mongolia (Barremian-Aptian) include representatives of that family that are close in their characters to Baissobius A.Rasn., a still older form from the Early Cretaceous

(Neocomian) of Baisy in the trans-Baykal region (described as Apocrita incertae sedis, Rasnitsyn, 1975a), and testify that this insect also belongs to Dryinidae. Representatives of Dryinidae have been regularly identified among the younger Late Cretaceous faunas from Taimyr (Upper Cenomanian, Agapa; Santonian, Yantardakh) and Canada (Campanian, Cedar Lake) and are also known from the Eocene (Baltic amber; N. Ponomarenko, 1975a) and Miocene (Primor'e) deposits.

At Bon-Tsagan there have also been found Chrysididae, different subfamilies of which are represented in the faunas enclosed in the Upper Cretaceous resins from Taimyr and Canada (Cleptinae, Amiseginae) and in various Cenozoic faunas. Bethylidae have been found in various Upper Cretaceous resins from Taimyr and Canada beginning with the Cenomanian (Agapa), and in many Cenozoic occurrences. Scolebythidae have been identified only in the Late Cretaceous (Santonian) from Taimyr (Yantardakh) and Embolemidae - in Baltic amber of the Eocene age. No Sclerogibbidae or Plumariidae have been found in fossil state. Most of the families are widely distributed in recent faunas, but Bethylidae and Chrysididae alone are more or less abundantly represented. Embolemidae are known from the Holarctic and Neotropical (Chile) realms and from Australia, Scolebythidae - from the major realms of the Southern hemisphere (the Neotropical regions, South Africa, including Madagascar, and Australia), and Plumariidae - from South America, South Africa and from the Mediterranean realm.

Aculeata s.str. p.110

The Aculeata proper (Aculeata s.str.) are divided into the following two main groups: sphecoid (Sphecoidea and Pompiloidea) and vespoid (Scolioidea and Formicioidea). The features characteristic of the sphecoid group are: 1) The persistance of the pubescent hypopharynx; 2) The enlarged posterior lobes of the pronotum overlapping the stigmae (figs 169-177) (relatively weakly pronounced in Thopalosomatidae); 3) The persistance (in Ceropales Latr. from the family Pompilidae, fig. 160a, and in

Sphecoidea, fig. 160b) of the metapostnotum medially expanded backwards; 4) The appearance on hind limbs of a cleaning apparatus (fig. 161) composed of two brushes of hairs at the base of the first segment and, primarily, at the base of one of the spurs of the tibia; the brush on the spur may secondarily extend all along the spur, may be supplemented by a chitinous comb, or may disappear (as in Astata Latr.); in bees the two brushes are lacking (may have disappeared with the expansion of the first segment of the tarsus), but the chitinous comb on the spur is sometimes present; 5) The persistance in most forms of a large arolium with an orbicula that may attain half the length of the unguis; 6) The complete absence of forms with the first metasomal sternite joined to the second tergite and a flat tilted platform at the apex of the first sternite (the obliquely disposed platform is present in Argogorytes Ashm., a representative of Sphecidae, but it is uneven and coarsely sculptured in this form); the posterior margin of the first sternite is primarily thin, similarly to that of the next sternites; it is rounded and broadly overlaps the base of the second sternite (fig. 162a); 7) The laterotergites of the first metasomal segment (fig. 162a) are very rarely reduced in width to a marked degree, only when the abdomen is of the petiolated type; 8) The second valves of the ovipositor often (and probably primarily) are not sharply differentiated into the thin distal and thick proximal parts; their base does not seem to be stretched out forming a medial process, but may bear lateral processes articulated with the branches of the furcula (see fig. 147); 9) The type of prey (beetle larvae leading a confined existence) that was primary for Vespomorpha, has been secondarily lost; the instances of the search for the prey inside the substratum (in some Sphecidae) may also be secondary*. The assortment of victims is highly varied and

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* Hunting by some primitive Pompilidae for spiders that live underneath the bark, may be a primitive feature (Epipompilus Kohl. which develops in egg cocoons of spiders and may also ectoparasitize the spiders themselves; Evans, 1972).

includes predominantly insects and spiders living in the open. The prey is commonly transported into the nest that may be composed of several individual cells; only the wasps whose larvae develop on active hosts living in the open or in burrows, or (less often) on hosts that are always attacked and paralyzed in their own burrows, do not transport their prey. All the cases, where the prey is not transported, may be secondary (this is less probable in the case of Epipompilus).

The alternative characters of the vespoid group are as follows: 1) The pubescence of the hypopharynx is invariably reduced; 2) The humeral tubercles are primarily and commonly rather small; 3) The metapostnotum is not expanded medially, but, on the contrary, is more or less flattened out and may be almost imperceptible from the outside (figs 160c and d); 4) If present, the cleaning device of the hind limbs has a different structure (the short brush at the base of the spur is lacking; for more detail see Brothers, 1975); 5) A more or less large arolium has been found only in the Late Cretaceous Falsiformicidae, but even in these forms the orbiculum may have been shorter than half the length of the unguis; 6) The first metasomal sternite (figs 162b-1) invariably appears to have a thicker posterior margin than that of the next sternites; the margin is either straight or notched and does not overlap the base of the second sternite; the posterior corners of the first sternite are not articulated with the second tergite only in the most primitive groups (Sierolomorphidae, Falsiformicidae, Sapygidae and in some representatives of Tiphiidae and Scoliidae); the flat tilted platform is a wide-spread character among Scolioidea (in many Tiphiidae and Multillidae; a rudiment of this platform is present in the males of Sapyginae) and has also been encountered in Vespoidea (Polistes Latr.) and in ants (Dorylus F.); 7) The laterotergites of the first segment remain broad only in the more primitive groups lacking the articulation between the first sternite and the second tergite; 8) The second valves of the ovipositor are commonly (and probably primarily) composed of a basal and a distal division that are distinctly differentiated by thickness, often bear a clearly

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defined medial process at the base, and appear to be always lacking the paired processes articulated with the furcula (fig. 147); 9) Most Scolioidea retain the primary type of their prey (the larvae of beetles living in the soil or in decayed wood); the scolioids which changed to a different type of prey, nevertheless search for it in shelters; this is also characteristic of many primitive ants (particularly among Ponerinae); Vespoidea alone prey almost exclusively on insects living in the open. Transportation of the prey is characteristic only of vespoids and ants, but is a very weakly developed practice among Scolioidea; nests with individual cells are characteristic only of Vespoidea.

Brothers (1975) believes that the position of the suture of the metapleuron is also an important character; the suture is oriented forward from the fossa (the exit of the apodema) located at the posterior margin of the sclerite (fig. 163). In his opinion in the primary state the fossa is in contact not only with the posterior, but also with the anterior margin of the metapleura and the suture mentioned earlier is lacking; in the intermediate state the suture is present and is oriented straight forward; and in the extreme state representing a synapomorphism of Sphecoidea, the suture is oriented downwards and extends as far as the fossa above the base of the metacoxae. In reality the last state which is very wide-spread in Ichneumonoidea and Evaniomorpha, is rather the primary plesiomorphic state. Furthermore, among Aculeata it is not restricted to Sphecoidea, but has also been encountered in Pompilidae (fig. 163b), Vespidae (fig. 163c), Sapygidae (Sapyga clavicornis L., S. similis F.) and Tiphiidae (Pterombrus rufiventris Cress.). Therefore this character cannot be used for distinguishing the sphecoid group from the vespoid group.

The proposed division of Aculeata s.str. into the sphecoid and vespoid groups differs from the system introduced by Brothers (1975) in that Brothers includes Pompiloidea into his superfamily Vespodea. He admits that reliable synapomorphisms of Pompilidae and Rhopalosomatidae with the other vespoids (within

the limits of his definition) are not known and lists those that are less reliable as follows: 1. Propleura closed throughout their length; but even in Sphecoidea the propleura are very rarely forced more or less widely apart by the prosternum (e.g. in Apis L.) and it may be a secondary development. Propleura that are closed (in contact) or very slightly open at the top (not more than in Ceropales) are more common. 2. Shortened (widely spaced) sclerites of the prepectus (i.e. the postspiracular sclerites, to use the terminology accepted in this work); but first of all, it is far from obvious that postspiracular sclerites that are in contact (as in many Chrysidoidea) are primitive (they are widely spaced in the lower Hymenoptera and in Stephanidae; fig. 123a), and, secondly, there is no reliable evidence that the mesothoracic margin outcurved in Sphecoidea in the form of a semicrescent, is homologous with these sclerites. 3. The metathorax is not raised anteriorly, but this is a primitive characteristic. 4. Reduction of the veins A(=A_2) and J in the posterior wing; but these veins are also found rarely in Sphecoidea, particularly J, while rudiments of A_2 have also been recorded in Scolioidea. 5. The deep axillary incision separating the jugal lobe of the posterior wing; but it is also characteristic of many Sphecoidea. 6. A similar structure of the genitals in Pompilidae and Sierolomorphidae; but the specific features in which they are similar, are not indicated, and we have not succeeded in detecting them in our material. 7. Closely spaced basal hooklets of the posterior wing; but, first of all, it is far from obvious that this character is apomorphic (in the lower Hymenoptera there have been established three groups of hooklets: the denser basal and distal groups and the more widely spaced median group; among the higher Hymenoptera, the basal group has been encountered, for example, in Ichneumonidae, Braconidae and Trigonalidae, in addition to Aculeata, while the medial group that is more characteristic of Aculeata, is there rare) and, secondly, some representatives of Sphecoidea also have closely spaced hooklets (Sphex L., Sceliphron Klug), even though they are disposed in these forms more distally than in Pompiloidea. 8) The small pterostigma; but it is highly variable in size even among Pompilidae, where there have also been

encountered medium-size pterostigmas (see the photographs in Townes' work, 1957). 9) Reduction of the denticles in larval mandibles to three or fewer; but it is also characteristic of bees. The similarity of Pompiloidea to the vespoid group thus proves to be much less profound than their resemblance to Sphecoidea, which supports the traditional view that Pompiloidea are close to Sphecoidea. p.113

Figs. 160-163

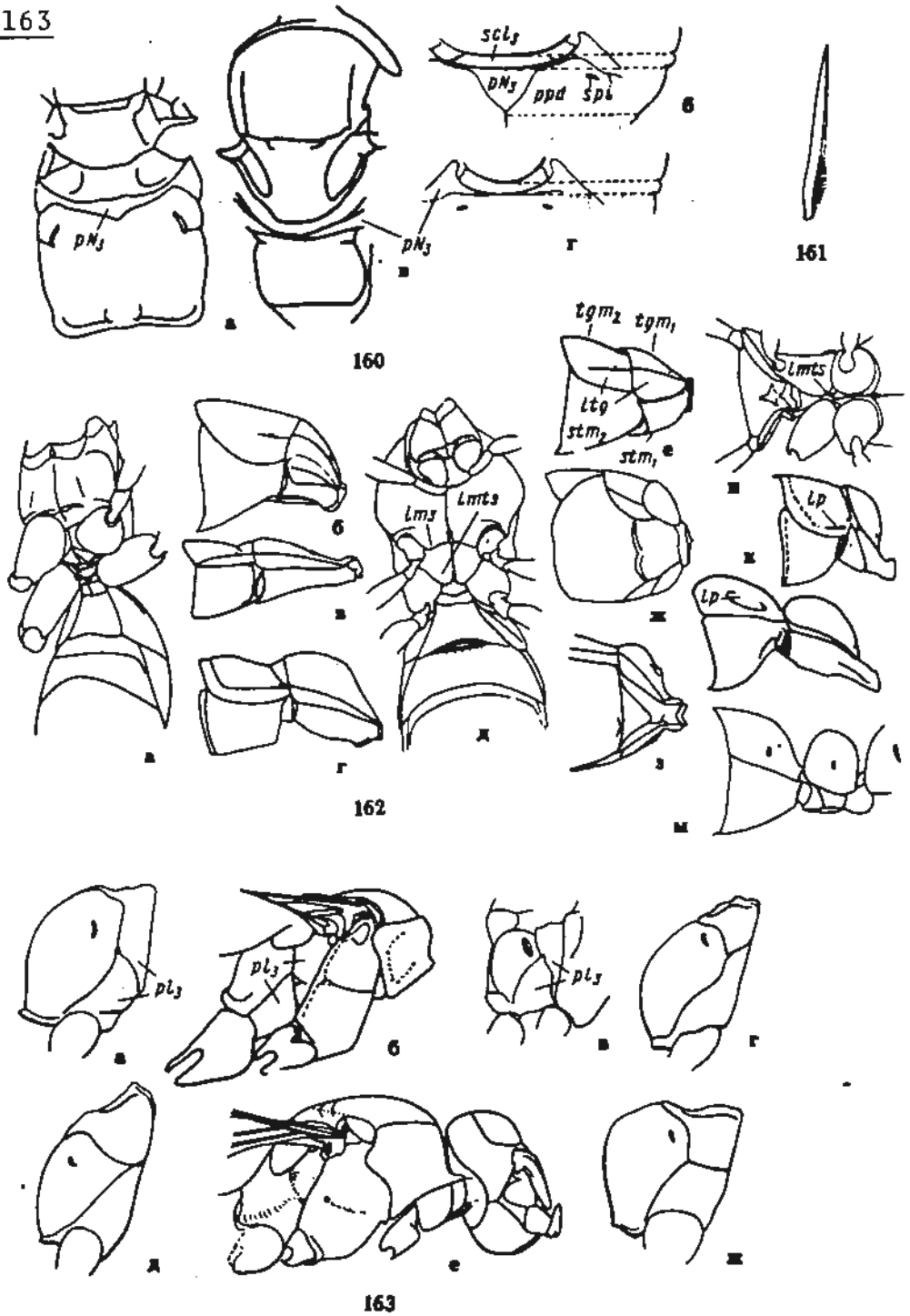

Fig. 160
Metapostnotum
a-Ceropales maculata F., Pompilidae; b-Cerceris sp., Sphecidae; c-Brachycistis carinata Fox; d-Methocha sp., Tiphiidae (a and c-original drawings; b and d-from Brothers, 1975).

Fig. 161
Cleaning spur of the hind tibia in Pepsis sp., Pompilidae (Brothers, 1975).

Fig. 162
The base of the metasoma viewed from below and in lateral view. a-Cryptocheilus versicolor Scop., Pompilidae; b-Cosila chilensis G.-M., Tiphiiidae Anthoboscinae; c-Scotaena paraguayensis (Schrottky), Tiphiidae Thynninae; d-Rhagigaster nigritulus Turner; Tiphiidae Thynninae; e-Proscolia archaica A.Rasn., Scoliidae Proscoliinae; f-Fedtschenkia grossa Sauss, Sapygidae Fedtschenkiidae; g-Pelochrum rapandum Spin., Sapygidae Sapyginae; h-Myrmosa melanocephala F., Mutillidae Myrmosinae; i-Pseudophotopsis incerta (Rad.), Mutillidae Pseudophotopsidinae; j-Bradynobaenus gayi Spin., Bradynobaenidae Bradynobaeninae; k-Apterogyne mlokosiewitzi Rad., Bradinobaenidae Apterogyninae; l-Dorylus sp. (o) Myrmicidae (original).

Fig. 163
Metapleura
a-Cerceris sp., Sphecidae; b-Ceropales maculata F., Pompilidae; c-Vespa orientalis L., Vespidae; d-Pseudophotopsis sp., Mutillidae; e-Anthobosca sp., Tiphiidae; f-Proscolia archaica A.Rasn., Scoliidae; g-Trielis sp., Scoliidae (a,d,e and g-from Brothers, 1975; b and c-original drawings; f-from Rasnitsyn, 1977c).

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The sphecoid group of superfamilies

Pompiloidea (figs 167-170) and Sphecoidea (fig. 171-177), the two distinctly segregated superfamilies of the sphecoid group,

have the following characteristics.

Pompiloidea: pronotum invariably extending as far as the tegulae, with free rounded or gently pointed lower corners that do not extend onto the lower surface of the thorax; posterior margin of the pronotum is not notched anteriorly of the humeral tubercles and may even project backwards (in Rhopalosomatidae), as is the case in many Scolioidea. Mesapleura with one single thin oblique suture or without the suture. Mesothorax does not protrude backwards at the bottom inbetween the mesacoxae, but may form backwardly projecting lamellar or (in Rhopalosoma, Ceropales) lobular processes of the postepisterna above the base of the mesacoxae. The latter are closed, with a slender tubular base. Metathorax flat. Metaposnotum moderately or (in Rhopalosoma) very short, less often gently expanded in the middle. Legs well-proportioned. Posterior wing with closely spaced basal hooklets or with the free end of A_1 reduced to varying degrees. Preying on spiders (Pompilidae) or Orthoptera (Rhopalosomatidae). Moreover, the larvae of Rhopalosomatidae and of some Pompilidae (Homonotus and many Ceropalinae) develop as parasites of active hosts. The other Pompilidae commonly paralize their prey, then transport it to their nests that are built before or after the preying (in the latter case the nest is always unicellular, in the former case it is commonly multicellular). Instead of the nests they may use shelters that are already there. Some Pompilidae lead a sleptoparasitic mode of existence. The major publications on biology of Pompiloidea are summarized in the work by Evans and West Eberhard (1970) and in the work by Iwata (1976).

Sphecoides: pronotum almost always ending short of the tegulae; its posterior margin is notched anteriorly of the humeral tubercles and its bottom corners are stretched out and almost meet on the lower surface of the thorax*. Mesapleura

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* With the exception of Dolichurus (personal communications by V. Pulavskii).

usually and probably primarily bear several rough sutures. Mesothorax often protrudes inbetween the mesacoxae (in Ampulex and in many bees it has a straight posterior margin). Mesacoxae more or less spaced out and with a broad base. Metathorax is raised inbetween the coxae in the form of a platform or at least of a longitudinal keel. Metapostnotum markedly elongated medially forming the "disc of the propodeum". Legs more or less short. Posterior wing very rarely (in some Sphecinae) bearing closely spaced hooklets that are disposed somewhat more distally than in Pompiloidea; the free end of A is commonly present. The assortment of hosts of Sphecidae is very large (various terrestrial anthropods), but they rarely include the larvae of insects with complete metamorphosis; the bees provide their larvae p.114
with pollen and nectar. The nest is almost always built before catching the prey and is commonly multicellular. Prionyx Vander Linden and Podalonia Fernald alone build their nests after seizing the prey. Some Sphecoidea use ready-made shelters. Chlorion maxillosum Poiret and Larra spp. develop as ectoparasites of active hosts living in burrows (i.e. of crickets and mole crickets, respectively) but in spite of its seemingly primitive nature, this mode of development is probably secondary. According to Malyshev's observations (1966), Larra anathema Rossi sometimes attempt to carry their prey, which is not characteristic of true ectoparasites. It is even less probable that this mode of life is primary for Ch. maxillosum, since the other species of this genus have a biology that is more typical of fossores (Sphecidae) (Bohart, Menke, 1976). Apparently the development on Grylloidea which live in burrows, is in itself a factor contributing to the transition to the secondary ectoparasitism of active hosts (another example of this type of changeover is the scolioid form Diamma bicolor Westw. from Tiphiidae Thynninae; Clausen, 1962). The data and literature on biology of Sphecoidea are summarized in the work by Iwata (1976) mentioned earlier, and those on fossorial wasps in the work by Evans and West Eberhart (1970).

Pompiloidea are generally much more primitive than Sphecoidea, but neither of their / two families can lay claim to being the ancestors of Sphecoidea because of the narrow base of their posterior coxae. Furthermore, Pompilidae have reduced stemming plates of the ovipositor and a distinctive structure of male genitals with long dorsal processes of gonocoxites, and Rhopalosomatidae have a specialized venation and markedly expanded tarsi in their families. The Early Cretaceous (Neocomian) Baissodidae (figs 164-166), particularly such as Baissodes A.Rasn. from Baysa in the trans-Baykal region may be more probable candidates for that role. Baissodidae, the oldest Aculeata s.str., were described by Rasnitsyn (1975a) as a family of an obscure taxonomic position mainly because of their extremely primitive assortment of characters, including the proximal position of the transverse 1m-cu near the base of the 2rm cellule (it is known only in some Sphecidae and in very few of the lower Tiphiidae) and a full complement of mesothoracic sutures (in all the other Aculeata the median suture is reduced or incomplete and is in the form of a thin line rather than furrow). It cannot be ruled out that Baissodidae were the common ancestor of all the Aculeata s.str., although their enlarged humeral tubercles (in Oryctobaissodes A.Rasn.and, to a lesser extent, in Baissodes) testify rather to their belonging to the sphecoid branch. New collections from Bon-Tsagan in Mongolia (Late Neocomian-Aptian have altered in many ways our notions of the evolution of various Hymenoptera and allowed us to define them more precisely. Even though these collections included no Baissodidae, they showed their direct relationship with Sphecoidea and helped us locate on the propodeum of the holotype Baissodes robustus A.Rasn. (see fig. 164) structures resembling the elongated metapostnotum with a longitudinal furrow characteristic of sphecids from Bon-Tsagan. The absence of the cleaning apparatus on the hind legs of Baissodidae (B. robustus in particular) or at least its extremely weak development in these insects may be an argument against referring Baissodidae to Sphecidae or even to Sphecoidea. However, this evidence is not unambiguous, since it may also be

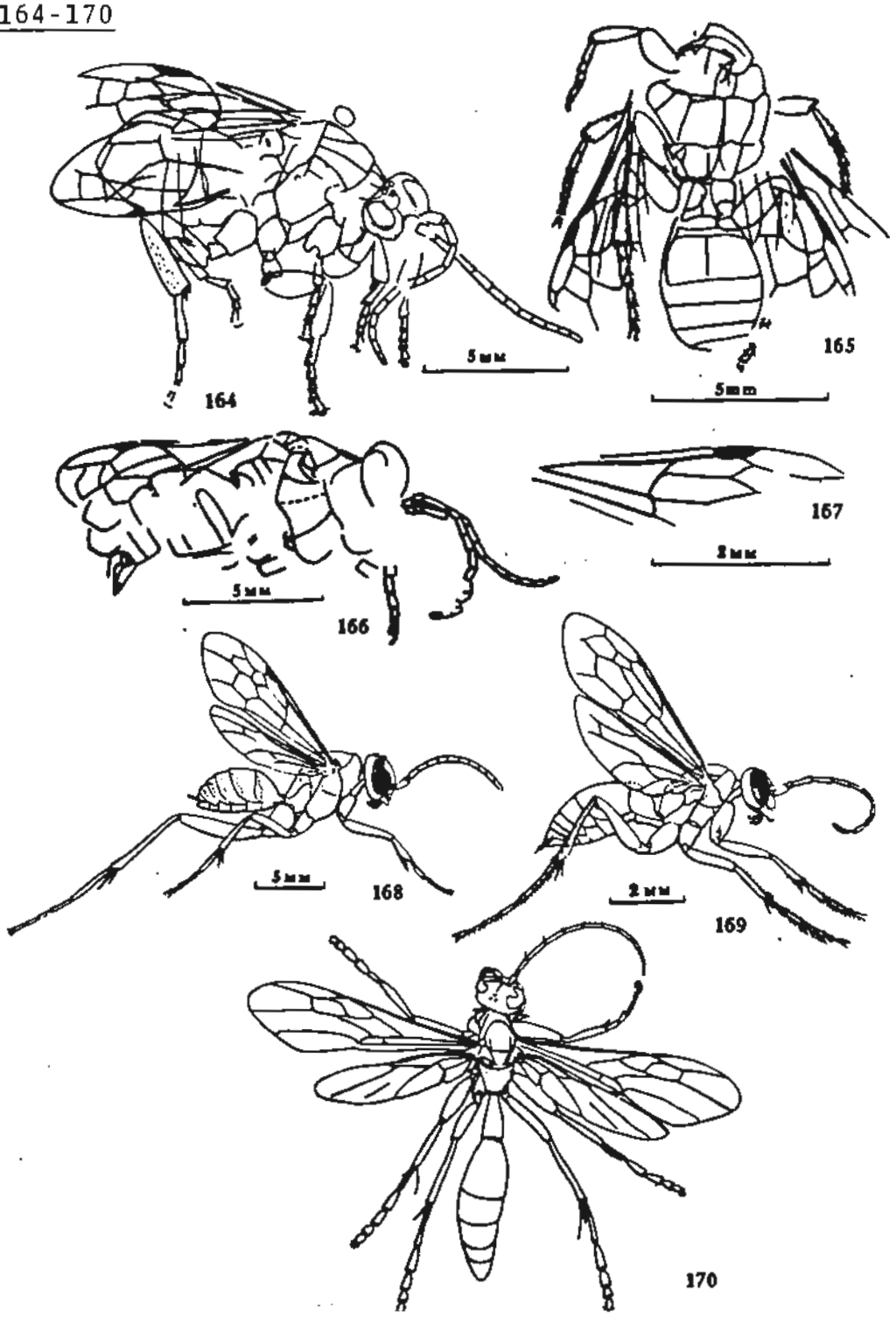
too weakly developed in fossorial wasps (Sphecidae) to be identified with confidence even from very well-preserved impressions. Baissodidae are therefore treated here as a group that is definitely ancestral to Sphecoidea, possibly ancestral to the sphecoid branch as a whole, and may be ancestral to all the Aculeata s.str.

Pompiloidea, one of the two superfamilies of the sphecoid branch, is composed of the families Pompilidae and Rhopalosomatidae. Despite their great species diversity and world-wide distribution, Pompilidae (figs 167-169) are uniform with regard to their morphology and biology. Fossil Pompilidae have been found in the Early Cretaceous deposits from the trans-Baykal region (Baisa, Neocomian) and Mongolia (Bon-Tsagan, Late Neocomian-Aptian) and have been identified among various Paleogene and Neogene faunas. Rhopalosomatidae (fig. 170) are a small group comprising a mere four genera, but are highly varied from the morphological viewpoint. The relationship between the type genus and their three other genera (Olixon Cam./=Nealgoa Brues/, Algoa Brues and Harpagocryptus Perkins) was subject of a lengthy controversy (Perkins, 1908; Brues, 1922; Reid, 1939; Townes, 1957; Riek, 1970b; and Brothers, 1975). It may, however, be now regarded as proven that they all belong to the same family (with the following main common characters in common: tarsi of the females enlarged; obliquely oriented suture of the metapleura lacking; lobules of the postepisternum present above the mesacoxae; ectoparasitic development on active Orthoptera living in trees with formation of a hard capsule made of discarded larval cases). p.116

As was mentioned earlier, we divide the superfamily Sphecoidea (fig. 171-177) into two families: Sphecidae and Apidae. In the literature this group is commonly divided into two superfamilies, one of which (Sphecoidea) comprises one single family, while the other one (Apoidea) is subdivided into several families. Arguments against this system can be found in Brother's work (1975). This author accepts, however, that Sphecoidea comprise a large number of families. We feel that it is also irrational, since it deprives us of the possibility to express taxonomically the distinctly discrete nature of fossorial bees and wasps (Brothers suggests that

they be treated as "informal groups" under the names of Spheciformes and Apiformes, but this is not the optimal solution to this problem), as well as because the differences between the "families" appear to be (at least at the intuitive level of assessment and in the absence of well-developed objective methods of measuring taxonomic differences) more superficial than those between the other families of Aculeata.

Figs. 164-170



Figs. 164-166
Representatives of the family Baissodidae (trans-Baykal region, Early Cretaceous)
164-Baissodes robustus A.Rasn; 165-Oryctobaissodes armatus A.Rasn.; 166-Trichobaissodes antennatus A.Rasn. (from Rasnitsyn, 1975a; 164-modified).

Figs. 167-170
Representatives of the superfamily Pompiliodes, families Pompilidae (167-168 and Rhopalosomatidae (170); 167-Pompilopterus ciliatus A.Rasn.; Lower Cretaceous of the trans-Baykal region; 168-Ceropales sp.; recent; 169-Cryptocheilus sp.; recent; 170-Rhopalosoma sp.; recent (167-from Rasnitsyn, 1975a; 168 and 169-from Riek, 1970b; 170-original drawing).

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The relationship of Sphecidae and Apidae appears to be that of the ancestor and its descendant. Brothers lists, for example, only the following synapomorphisms of fossorial wasps in relation to bees: in the fossores the pronotum invariably ends short of the tegulae and the exterior of the middle and posterior tibiae bears moderately well-developed spines, whereas in the bees the contact between the pronotum and the tegulae may persist and the spines on the tibiae are weak. The latter difference is fairly minor and the former one is somewhat inaccurately stated: the tegulae and the pronotum are in contact in Dolichurus and in some Pemphredoninae. The ancestor of the two families (i.e. the insect with these characters in the plesiomorphous state, but similar in all the other respects to Sphecidae) undoubtedly deserves being referred to that family, which suggests that bees descended from fossorial wasps. The exact time when the bees diverged is not known. It may be tentatively estimated from the following facts: a)fossorial wasps appeared in the Neocomian; and b)the earliest finds of bees as such have been recorded in the Eocene (Baltic amber). The appearance of bees was associated first of all with gathering of pollen and nectar

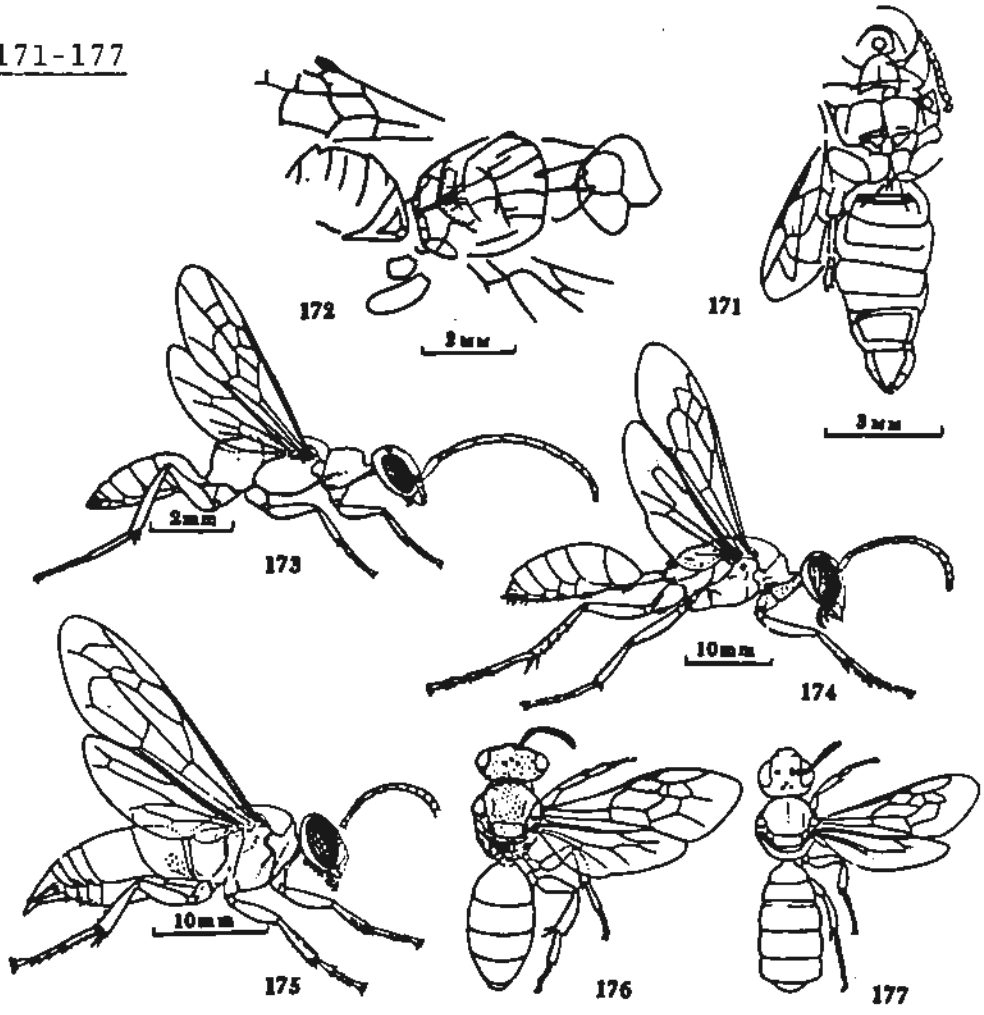
instead of preying on insects, and with appropriate morphological and biological modifications such as the plumose pubescence, the enlargment of the first segment of the posterior tarsus and the loss of the cleaning apparatus on the hind limbs; we can also include here (though with less confidence) the elongation of the labiomaxillary complex, the change to mass provisioning of the nest instead of its provisioning in one single operation, and construction of the nest prior to gathering food, since the same characters are found in most fossorial wasps. Some of the synapomorphisms of bees have no obvious relation to the changes in their trophic specialization (e.g. the loss of the interlobar septum of the seventh tergite in females).

The paleontological history of Sphecoidea and of fossorial wasps (Sphecidae) in particular, begins in the Early Cretaceous. Many of the oldest wasps, including those described from the Neocomian of Great Britain (Archisphex Evans) and of the trans-Baykal region (Angarosphex A.Rasn. and Cretosphex A.Rasn., figs. 171-172) turned out to be representatives of Sphecidae. This supports Evans's hypothesis (1969) regarding the former genus, but contradicts the views which we held in the past, when we set Angarosphex apart as a separate family (Rasnitsyn, 1975a). We have been able to correct this thanks to the new collections from the Late Neocomian-Aptian of Mongolia. In the course of these collections we discovered a rich fauna of wasps that are obviously close to the three genera mentioned above, yet have features characteristic of fossores, such as the specific shape of their pronotum (including the stretched-out and nearly converging lower corners) or their markedly expanded backwardly metapostnotum. This seems to be a grouping ancestral to the other Sphecoidea, but of a thus far obscure taxonomic status. It could be included p.117
into the subfamily Ampulicinae on account of the long pronotum and strongly developed notaulae of its representatives, but there are more reasons to believe that the forthcoming detail analysis of this group will show it to be a separate family.

The characteristic features of the subsequent history of Sphecoidea is the absence of their representatives (excepting

Pemphredoninae) throughout the Late Cretaceous, which cannot be explained by taphonomic factors alone (the bulk of our material has been derived from small lumps of fossil resins, where the probability of finding small insects associated with trees is particularly great, but Pemphredoninae are not the only representatives of Sphecoidea characterized by this mode of existence),and the predominance of social Apinae throughout the Paleogene, during which primitive bees were rare. Zherikhin (1978) advanced the hypothesis that the latter may be due to the relative scantity during the Paleogene of wide-open spaces, which are the principal habitats of solitary bees.

Figs. 171-177



Representatives of the superfamily Sphecoidea, families Sphecidae (171-175) and Apidae (176-177)

171-Cretosphex incertus A.Rasn.; 172-Angarosphex myrmicopterus A.Rasn.; 173-Aphelotoma sp.; 174-Aphex sp.; 175-Sphecius pectoralis (Smith); 176-Sphecodes gibbus (L.); 177-Ceratina cyanea (Kirby); (171-172-trans-Baykal region; Early Cretaceous; from Rasnitsyn, 1975a; 172-modified; all the others are recent forms; 173-175-from Riek, 1970b; 176-177-from Bouěk, Sostera, 1957).

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The vespoid group of superfamilies p.118

As was mentioned earlier, Brothers (1975) rejected most of the generally accepted superfamilies of Aculeata s.str. and united Vespoidea, Formicoidea, Scolioidea and Pompiloidea within the same superfamily. His Vespoidea form two main stems, one of which includes Tiphiidae, Sapygidae and Muttilidae, while the other one comprises Sierolomorphidae, Pompiloidea, Bradinobaenidae, Formicoidea, Scoliidae and Vespoidea (the taxa are listed in the order of their divergence according to Brother's scheme, but with the size and rank accepted in this work). This scheme of phylogenetic relations does, indeed, complicate the institution of traditional superfamilies, but it is difficult to agree with this scheme. First of all it is much more probable that Pompiloidea are phylogenetically closer to Sphecoidea than to Scolioidea and particularly to Sierolomorphidae and Bradynobaenidae, as Brother's scheme suggests. The find of a primitive Scolioidea from the subfamily Proscoliinae (Rasnitsyn, 1977c) has shown that the similarity between Scoliidae and Verspoidea is also superficial or at least that it has been acquired independently (see more details farther on). We cannot rule out that Formicoidea and Vespoidea may be close to Bradynobaenidae, but it is less likely than their being close to Sierolomorphidae and extinct Falsiformicidae. If we take into account these and certain other corrections, Scolioidea turn out to be a much more homogenous group.

The structure of the vespoid group is not examined here in detail: Vespoidea anf Formicoidea may have descended directly from Scolioidea, and it is impossible to discuss the relationships of the three superfamilies prior to analyzing the system and phylogenesis of Scolioidea themselves. The group, i.e. primitive Scoliidae and Masaridae Euparagiinae, appear for the first time in the paleontological record in the latter half of the Early Cretaceous (Late Neocomian-Aptian of Mongolia, Bon-Tsagan).

The superfamily Scolioidea

The size of the families referred to Scolioidea (figs. 178-192) is here the same as in Brothers's work (1975), but their relationships appears to us to be somewhat different. The differences in our views are due to a significant extent to the following: Brothers believes that the raised platform in the middle of the metathorax which spreads apart the mesocoxae (fig. 193), is a plesiomorphous character, whereas our data suggest that it is rather an apomorphous state. Indeed, among the Hymenoptera that do not belong to Aculeata, the metathorax is commonly and primarily flat. A flat metathorax has been found among the aculeate insects in many Chrysidoidea, Pompiloidea, ants, social wasps (Vespidae) and in some Scolioidea (Sapygidae, Sierolomorphidae, and, probably, Falsiformicidae; as will be demonstrated later on, an analogous condition appears to have arisen secondarily in Mutillidae and Tiphiidae Methochinae). A raised platform or a longitudinal crest is characteristic of the group Chrysididae+Bethylidae+Embolemidae and of the females of Plumariidae among Chrysidoidea, as well as of Sphecoidea and many Scolioidea, excepting the families listed above. In the case of Chrysidoidea there are reasons to believe that Plumariidae acquired the metathoracic platform independently of the other families (see above). The structure of the metathorax in Scolioidea provides even more grounds for this assumption. In Tiphiidae this platform has a highly characteristic triangular shape; moreover the base of the triangle bearing two lobules adjoins

anteriorly the posterior coxae, while its apex is located markedly below the level of the mesothorax; at the same time analogous, but larger mesothoracic lobules are present above the base of the mesocoxae. The metathoracic platform, as well as the mesothoracic lobules may be reduced. If this is the case, their rudiments may nevertheless persist. Particularly clearly defined vestiges of the platform have been recorded in females of Mutillidae of the genus Pseudophotopsis André (see fig. 162i). The structure of the thorax in Scoliidae with its markedly expanded platform forcing the meso- and metacoxae widely apart (as a result of which the lobules of the mesa- and metathorax become less pronounced, but do not disappear), may also be derived from the condition characteristic of Tiphiidae. On the other hand it is fairly difficult to derive the platform of Bradynobaenidae (which has parallel sides and a blunt anterior margin; that margin cuts into the mesothorax and is disposed at the same level as the latter; the lobules of the mesothorax, as well as those along the posterior margin of the platform are lacking) from the platform of Tiphiidae or, conversely, to regard it as the structure from which the latter originated. Bradynobaenidae reveal a considerably greater, though distinctly secondary similarity in this character to some of the bees, particularly Hylaeus F. p.119

It appears more probable that the mesothoracic platform evolved independently in Bradynobaenidae, Tiphiidae, Sphecoidea and Chrysidoidea. This is suggested not only by the differences in its structure, but also by the absence of any traces of this platform in many of the primitive aculeate insects (Scolebythidae, Pompilidae and Sierolomorphidae) and in descendants of primitive Scolioidea, i.e. in ants and in Vespidae.

In his later work Brothers (1976) mentions a new point of resemblance between Scoliidae and Vespidae: their strongly developed metathoracic phragma. Analysis of additional material shows, however, that this character is equally unreliable (fig. 194). The metathoracic phragma is, indeed, very strongly developed, but has a different structure in Scoliidae and Vespidae. In Scoliidae the phragma is very long not only

on the sides, but also in its middle portion, from which the muscle diverges towards the mesothoracic phragma (the lateral segments are occupied by the powerful muscles extending onto the anterior wall of the mesothoracic scutellum, but no such muscles have been found in Vespoidea). In Vespidae the metathoracic phragma is very narrow in the middle (Polistes sp., Ceramius caucasicus Andre) or discontinues altogether (Ancistocerus sp., Vespa crabro L.); moreover in hornets (Vespa crabro L.) its halves thin out medially, whereas in Ancistrocerus they merge with the exterior of the propodeum, but remain relatively broad. The muscles extending onto the mesothoracic phragma are disposed laterally and are attached to the phragma considerably closer to its anterior edge than in Scoliidae. In Scolioidea the structure of the phragma is highly variable. Moreover, in Sapyga it bears a very close resemblance to that of Polistes, much closer than the resemblance of any Vespoidea to Scoliidae.

The structure of the recently described Proscolia archaica A.Rasn. (Scoliidae, Proscoliinaem Rasnitsyn, 1977c; see Fig. 162e, 163f and 183) also provides weighty arguments against Brothers's scheme. It shows that the similarity between Scoliidae and Vespoidea in characters such as the long clypeus, gemmiform eyes, elongated labiomaxillary complex at the expense of the glossae and paraglossae, membranized pterostigma, and the distant position of the entry of the metapleural apodema relative to the mesopleura, manifests itself only in the higher Scollidae and does not prove that Scoliidae and Vespoidea are closely related. The other characters in which Scoliidae are said to be close to Vespidea, sometimes also to ants and Bradynobaenidae (Brothers believes all these groups to be related) are also less than reliable: the pointed and seemingly immobile corners of the pronotum and the completely invaginated prosternum that is imperceptible from below, are found among Bradynobaenidae only in their type genus and therefore arise here independently; as Brothers himself points out, the projection of the posterior corner of the pronotum above the tegula differs in appearance in Scoliidae and Vespidae (some ants, particularly Dorylinae, are considerably closer to Vespoidea in this respect),

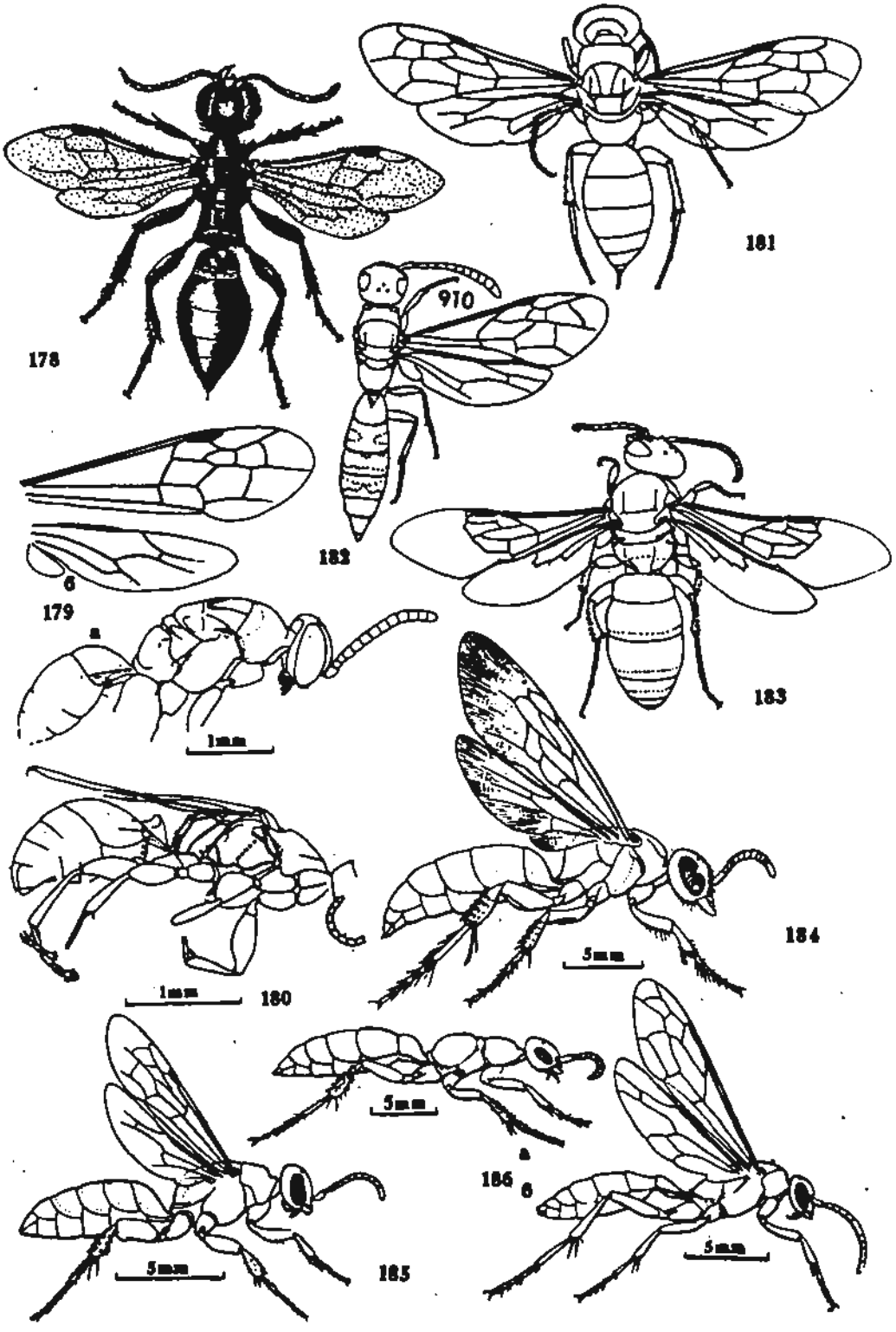
which may be interpreted as evidence of an independent development of this character from a more primitive condition characteristic of the lower Scolioidea. Of course, all these characters remain significant, but we feel that the attributes discussed below, in which Scoliidae resemble Tiphiidae, are more substantial.

The most important factor making it impossible for the author to fully agree with Brothers's scheme, is the distribution of some of the characters which Brothers failed to take into account or did not analyze thoroughly enough. We are referring first of all to the region of articulation of the two first segments of the metasoma, where Scolioidea have another highly mobile articulation that is also found in many other Apocrita, but is developed more intensively in Scolioidea than anywhere else. The reason for its development may have been the need to provide the metasoma with an adequate degree of mobility for injuring the prey p.121
in narrow crevices of the substratum. This process of optimization occurred in different groups in a parallel fashion and independently of one another with regard to details but it distinctly followed two main trends.

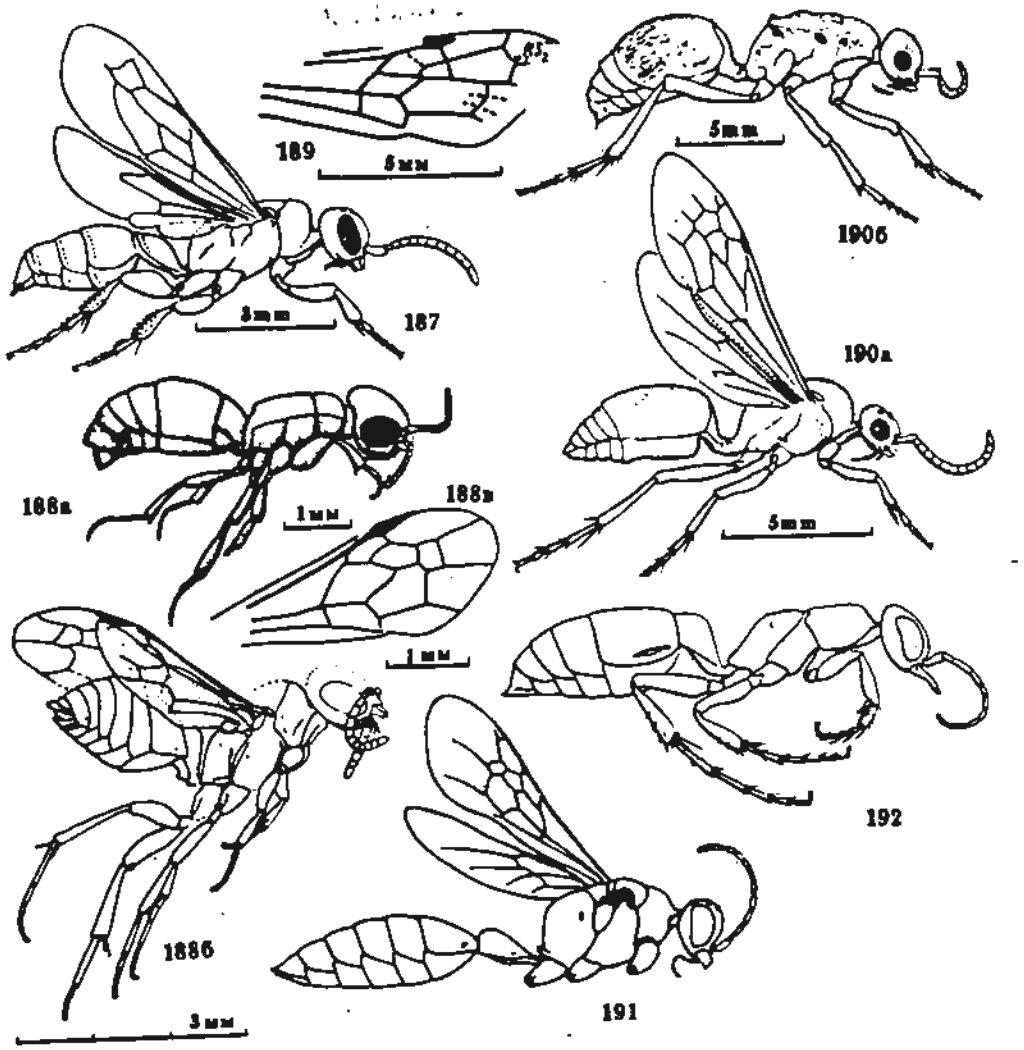
The most common way of increasing the mobility of the metasoma was to increase the amplitude of its vertical movements. The primary condition where the first sternite broadly overlapped the base of the second sternite (see fig. 162a), was already lost in the ancestor of Scolioidea. The females of p.122
Sapyginae, particularly (among the material to which the author has access) those of Polochrum repandum Spin. (see fig. 162g), have a primitive appearance with regard to this characteristic. The modified first sternite in the males of Sapyginae and in those of Fedtschenkiinae (see fig. 162f), an even more primitive subfamily of Sapygidae, evidences, however, that its "primitive" character is here secondary. The most primitive structure is found in Tiphiidae Anthoboscinae and Scoliidae Proscoliinae (see figs. 162b and e), where the first sternite had a gently concave profile, a convex cross-section, and a slightly notched posterior p.123
margin. The second sternite is also convex in transverse section, but less so than the first sternite, so that when the metasoma

straightens out the corners of the first sternite overlie the surface of the second sternite and its middle portion remains free (is not appressed) leaving open a crescent-shaped slit that is only partly covered by a slightly sclerotized membrane.

Figs. 178-186



Figs. 187-192



Representatives of the superfamily Scolioidea.
178-Sierolomorpha atropos Nagy, Sierolomorphidae; recent; 179-Taimyrisphex pristinus Evans, ♂, Falsiformicidae; Upper Cretaceous, Taimyr: a-Structure of the body; b-Wings; 180-Falsiformica cretacea A.Rasn., ♀, Falsiformicidae; Upper Cretaceous, Taimyr; 181-Fedtschenkia grossa Sauss., Sapygidae Fedtschenkiinae; recent; 182-Sapyga clavicornis (L.), Sapygidae Sapyginae; recent; 183-Proscolia archaica A.Rasn., Scoliidae Proscoliinae; recent; 184-Campsomeris sp., Scoliidae Scoliinae; recent; 185-Anthobosca sp., Tiphiidae Anthoboscinae; recent; 186-Diamma bicolor Westw., Tiphiidae Thynninae; a-Female; b-Male; 187-Tiphia sp., Tiphiidae, Tiphiinae; recent; 188-Protomutilla Bishoff, Mutillidae Myrmosinae:

a-P. megalophthalma Bishoff, ♀; b-P. sp., ♂, general view; c-P. sp., ♂, anterior wing; Upper Eocene from the Baltic region; 189-Cretavus sibiricus Sharov, Mutillidae?; Upper Cretaceous, Western Siberia; 190-Ephutomorpha sp., Mutillidae Mutillinae; a-Male; b-Female; 191-Typhoctes williamsi Krombein, Schuster, ♂; Bradynobaenidae; recent; 192-Typhoctoides aphelonix Brothers, ♀; Bradynobaenidae; recent; (178-from Nagy, 1971; 179a-original drawing, holotype; 179b-from Evans, 1973; 180 and 189-from Rasnitsyn, 1975a; 181-original drawing; 182-from Boucek, 1957; 183-from Rasnitsyn 1977a; 184, 187 and 190-from Riek, 1970b; 188a-from Brues, 1933; 188b-c---original drawing, specimens PIN N° 364/280-281; 191-from Krombein, Schuster, 1957; 192-from Brothers, 1970).

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Figs. 193-196

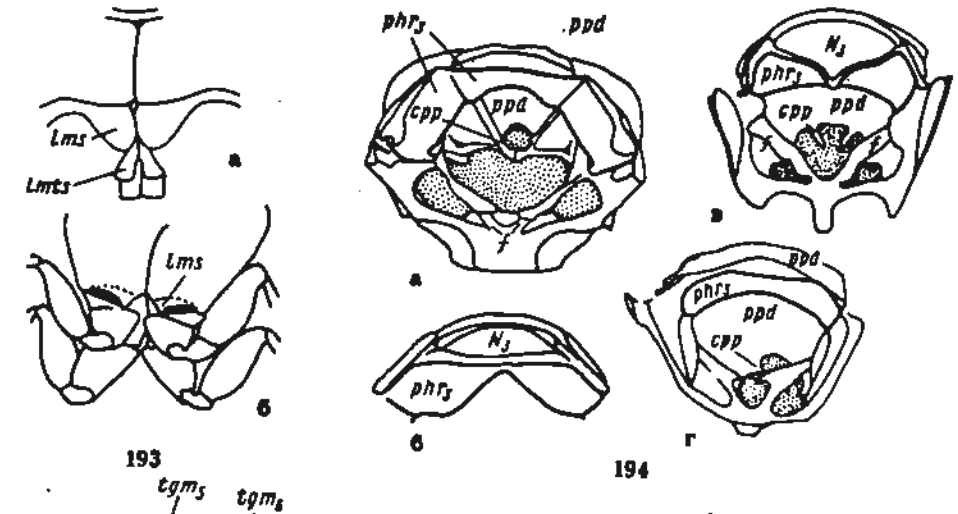

Fig. 193
Thorax viewed from below.
a-Cosila chilensis G.-M., Tiphiidae Anthoboscinae; b-Fedtschenkia grossa Sauss., Sapygidae Fedtschenkiinae (recent, original drawings).

Fig. 194
Posterior part of the thorax, interior view (the heavy line marks the boundaries of the third phragma)
a-Scolia maculata (Drury), Scoliidae; b-Polistes sp., Vespidae; c-Vespa crabro L., Vespidae; d-Sapyga similis (F.), Sapygidae (all recent; original drawings).

Fig. 195
The sixth metasomal sternite of a female
a-Podalonia hirsuta (Scop.), Sphecidae; b-Myrmecia gulosa F., Formicidae; c-Cosila chilensis G.-M., Tiphiidae; d-Pseudophotopsis incerta (Rad.), Mutillidae; e-Fedtschenkia indigotea Rad., Sapygidae Fedtschenkiinae; f-Polochrum repandum Spin., Sapygidae Sapyginae (all recent; original drawings).

Fig. 196
Male genitals
a-Anthobosca erythropyga (Burn.), Tiphiidae; b-Polochrum repandum Spin., Sapygidae; c-Typhictes peculiaris (Cress.), Bradynobaenidae (all recent; a-original drawing; b-from Tobias, 1965; c-from Krombein and Schuster, 1957).

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While the metasoma curls under, the base of the second sternite slides underneath the apex of the first sternite until its outcurved middle portion slips into the notch in the posterior margin of the first sternite. The sclerotized lamina of the closing membrane rests then on the basal surface of the second sternite. The next state may be observed in Tiphiidae of the subfamily Thynninae (see figs 162 c and d). The posterior edge

of their first sternite is straight and so is the base of the second sternite in transverse section; the gap between the sternites closed by the plate (lamina) of sclerotized membrane, persists, but alters in shape from falcate to more or less straight; at the base of the second sternite there appears at the same time a more or less wide transverse vallecula in which the posterior margin of the first sternite, together with the closing lamina, is lodged, when the metasoma is folded under. In many Thynninae the profile of the first sternite becomes outcurved (convex) or angularly prominent in the middle because of the appearance of a tilted platform at its apex; as a result of this the height of the posterior opening of the first segment decreases relative to the height of the segment as such, ensuring thereby the required capacity of the segment and providing for a great amplitude of vertical movements of the metasoma. The appearance of the tilted platform leads to a decrease in the vertical diameter of the articulation opening not only of the first, but also of the second segment. This is manifest in the markedly prominent (convex) profile of its sternite, as a result of which the segment rapidly increases in height posteriorly of the base. There appears a notch between the first and second sternites, which is a highly characteristic feature of most Scolioidea. This notch is lacking in Sapygidae in spite of the presence of the tilted platform in Fedtschenkiinae (see fig. 162f) and of its rudiment in male and some female representatives of Sapyginae. The base of the second sternite does not flatten out in Sapygidae, the posterior margin of its first sternite does not straighten out, and there appears no distinctly defined transverse vallecula at the base of its second sternite. The modifications along the lines characteristic of Tiphiidae and of a number of other Scolioidea appear to have occurred independently and in a parallel fashion in Sapygidae.

Further modifications involved in transferring the articulation between the posterior corners of the first sternite and the second segment from the second sternite to the second tergite (see figs 162 h-l), begin in Tiphiidae (Myzininae) and

attain their full expression in the higher Tiphiidae, Scoliinae and Mutillidae (in Myrmosinae this articulation is weakly developed). The same articulation appears independently in Bradynobaenidae, Formicidae and Vespidae. The transfer of the articulation to the second tergite precedes (in Methochinae and in the males of many Thynninae) the narrowing down of the laterotergites of the first metasomal segment.

Another development in Scolioidea that is roughly parallel to the displacement of the articulation from the sternite to the tergite of the second segment, is the nearly complete elimination of sliding movements between their sternites (only the rocking movement of the sternites relative to one another persists). At the same time the transverse vallecula at the base of the second sternite loses its function and becomes less distinct.

When the articulation of the basal segments of the metasoma develops along the latter trend, the mobility increases on account of both vertical and rotary movements. Their combined effect enables the metasoma to bend in a variety of planes, vertical as well as oblique. The initial stages of this development are illustrated by Sierolomorphidae and Falsiformicidae (see figs 179-180), where the structure of the first sternite remains almost the same as that of Anthoboscinae and Proscoliinae, except for the increased convexity of its cross section. The second sternite also becomes more outcurved (prominent) in transverse section; at the same time its base narrows down and there appears here a transverse vallecula similar to that observed in Thynninae. However, the "neck" of the sternite located anteriorly of the vallecula, increases in length unevenly or largely on the sides, but mainly in the middle, and is at an angle to the axis of the segment. When the metasoma is straight, this "neck" covers the slit underneath the margin of the first sternite, but when the metasoma begins to bend, its* margin slides along the p.124

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* It is not clear whether the author is referring to the margin (or edge) of the metasoma or to that of the "neck". Translator.

inner surface of the first sternite until the notched posterior edge of the latter meets the convex (in the transverse direction) bottom of the vallecula. The functional significance of the differences between this mechanism and the mechanism described earlier lies in that it permits the articulation to function normally when a segment turns relative to the other along their longitudinal axis.

A similar structure has also been observed in vespoids and ants, but it is complicated in these insects by the articulation of the corners of the first sternite with those of the second tergite and by narrowing down of the first laterotergites. In ants it is commonly complicated further by additional projections of the second sternite, by the fusion of the tergites with their sternites, etc. This condition persists in a rather primitive (at least superficially) form in Dorylinae (fig. 162l) and Leptanillinae. It is also characteristic of Apterogyninae (fig. 162m), but the other Bradynobaenidae are closer in the structure of their articulation to most Scolioidea (fig. 162j): the first sternite and the base of the second sternite are flat in the transverse direction; Bradynobaeninae and Typhoctinae (also some Chyphotinae, but less distinctly) exhibit a discrete tilted platform*; the vallecula at the base of the second sternite is narrow, the neck anteriorly of the vallecula is not expanded medially, although it may (in Chyphotinae) be markedly outcurved; the first sternite articulates with the second tergite. The similarity of Apterogyninae to Sierolomorphidae, Vespoidea and, particularly, Formicoidea with regard to the character of articulation appears to be a parallelism (an example of the opposite parallelism is demonstrated by the Vespoidea of the genus Polistes Latr. that are similar in the character of that joint to the higher Tiphiidae, Multillidae, etc.).

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* A rudiment of the tilted platform also appears to persist in males of . Apterogyninae.

Different structural variants of the sixth metasomal sternite are distributed in a similar manner, but more distinctly in females (fig. 195). The primitive shape of the sternite similar to that found in many Sphecoidea and Pompiloidea (more or less conical, with a round posterior aperture and with thinner lateral lobules separated from the main part of the sternite only by the drastically reduced thickness of the sclerite) persists in Sierolomorphidae (+Falsiformicidae?), Formicoidea and Vespoidea, but in the latter the sternite is often more or less flat at the bottom.

In most Scolioidea (Tiphiidae, Scoliidae and Bradynobaenidae) the sixth sternite of females is flat at the bottom, while its lateral lobules are enlarged, separated by an incision that commonly continues in the form of a desclerotized band, appressed and have a subhorizontal position; they may even overlap along the median line. As a result of this the opening through which the ovipositor emerges, acquires the shape of a more or less broad transverse slit providing freedom of lateral movements to the stinger. With the change-over to the development at the expense of relatively immobile types of prey, the freedom of movement of the ovipositor becomes less important and the opening decreases secondarily in size, but the primitive structure of the sternite does not become restored. These changes are characteristic of Sapygidae and Mutillidae, parasites or inquilines of Sphecoidea (secondarily also of other insects), but the two families achieve here similar results by different means, which testifies against Brothers's (1975) assumption that they are close. In Sapygidae the conical shape of the sternite becomes restored and the sternite itself increases in length, but the incisions separating its lateral lobules initially persist (in Fedtschenkiinae). On the other hand the characters persisting in Mutillidae are the flattened-out shape and relatively small length of the sternite, while its lobules adgrow secondarily, in the event of which the desclerotized band along their boundary is preserved.

Some features of male genitals in Scolioidea (fig. 196) also testify that Bradynobaenidae are close to the group

Tiphiidae-Scoliidae-Mutillidae-Sapygidae. A feature highly characteristic of Sapygidae and of many Tiphiidae (Anthoboscinae, Tiphiinae and some Myzininae) is the longitudinal suture separating the ventrolateral part of the coxite bearing the gonostyle, from its dorsolateral part. It is also characteristic of Bradynobaenidae of the subfamilies Typhoctinae and Chyphotinae, but no differentiation of this type has been observed in any of the other Aculeata. Given the unusual nature of this feature, a feature having no obvious functional significance (it lends no mobility to constituent parts of the coxite), its recurrent development is less probable than its appearance in the ancestor of the five families of Scolioidea listed above, and its subsequent loss in Scoliidae and Mutillidae, and in some members of Tiphiidae and Bradynobaenidae. p.125

This also applies to the "armament" of the tibiae, particularly the middle ones. In each of the five families which we believe to be closely related, there are and often predominate forms with transverse rows of thick spines on the outer surface of the tibia (figs. 181-192). The presence of this equipment is undoubtedly related to the digging activities: the spines are developed more strongly in female individuals, but grow weaker even in females when the digging activity of the insects declines (e.g. in Methochinae and in Pterombrus among Myzininae). The row of spines may be found, however, even in members of the groups, the biology of which requires no burrowing of passages in the substratum (Sapygidae Fedtschenkiinae, some Mutillidae and, particularly, Myrmosinae and Pseudophotopsidinae; Typhoctinae, Chyphotinae and Bradynobaeninae of Bradynobaenidae may also be cases in point, but the biology of this family is not known). This suggests that in the group of families discussed the absence of the row of spines on the tibiae is a secondary development.

In Sierolomorphidae and Falsiformicidae the spines not only do not form transverse rows, but are generally very weakly developed. Since the biology of these insects is unknown, the

weak armament of their legs means little by itself, but it is much weaker than that of most Scolioidea, as is also the case with the ants and social wasps, even though some of them dig fairly actively. The probability of a close relationship of the two latter groups to Sierolomorphidae and Falsiformicidae suggests that in this evolutionary branch as a whole, the powerful armament of the tibiae, unlike that of the branch uniting most Scolioidea, was not a primary condition and apparently did not develop even at later evolutionary stages because of the lack of some indispensable preconditions (for example, because the digging behaviour of this group, when it does arise, is different from that of most Scolioidea).

Biological data could be highly significant for clarifying the structure of the superfamily Scolioidea, but in the absence of any biological information on the families Bradynobaenidae and Sierolomorphidae, the most important families in this respect, we are compelled to make do with data on their morphology. However, as was demonstrated earlier, the morphology testifies rather in favour of the existence of two main evolutionary lines of Scolioidea, one of which leads to Bradynobaenidae, Sapygidae, Scoliidae, Tiphiidae and Mutillidae, and the other one to Sierolomorphidae, Falsiformicidae and farther on, probably to Vespoidea and Formicoidea. The attributes, in which some Bradynobaenidae resemble ants, may have arisen independently (the structure of the articulation between the first segments of the metasoma, as well as the deep constriction between the second and third segments in Apterogyninae; the upcurved stinger of Typhoctinae and Chyphotinae similar to that found in ants; and the distinctive structure of the pronotum and prothorax in Bradynobaeninae that was mentioned earlier).

The divergence of the former group representing the main stem of Scolioidea, was probably accompanied by the modifications described above [in the structure of the articulation of the basal metasomal segments (intensification of vertical movements in the articulation), of the sixth sternite in the females (flattening out with formation of a wide transverse slit at the apex of the metasoma) and in the male genitals (longitudinal

segmentation of the coxites)] and by the development of a powerful armament of the tibiae. This group also displays some characteristic common tendencies: the appearance of a raised platform on the metathorax, the elongation of the distal division of the stinger and the appearance of a sharp bend near its boundary with the basal division, and the development of denticles or lobes on the last sternite in males. Invagination of the metapostnotum is also characteristic of the members of this group in contrast to those of Sierolomorphidae and Falsiformicidae, but this feature is also characteristic of Vespoidea and Formicoidea that are close to the two latter families.

The time of appearance of the group Bradynobaenidae-Sapygidae-Scoliidae-Tiphiidae-Mutillidae is determined by the find of a primitive representative of Scoliidae (more primitive than Proscolia) in the Early Cretaceous fauna at Bon-Tsagan in Mongolia. The identification of the Late Cretaceous find that is next in time (Cretavus Sharov from the Turonian of Western Siberia, Bol'shoi Kas), as a representative of Mutillidae (Rasnitsyn, 1975a) no longer appears indisputable. Cretavus (fig. 189) has undoubtedly features in common with Mutillidae, but it is known only from an imperfectly preserved forewing and its resemblance to Mutillidae is incomplete. The classification of this insect with Mutillidae therefore raises certain questions. The report of a find of a Scolioidea in the Neocomian of the trans-Baykal region (Rasnitsyn 1975a) was erroneous: Oryctopterus A.Rasn., the form described from a wing fragment as a scolioid of an indeterminate taxonomic position, turned out to be a bug of a separate family close to Hebridae (identified by Yu.A. Popov). p.126

The sequence of divergence of the families forming the main stem of Scolioidea is not quite clear. Judging from the structure of the lower meso- and metathoracic surfaces and particularly from the presence of the mesothoracic lobules or their rudiments in Tiphiidae, Mutillidae and Scoliidae, these families form an integral group with Tiphiidae in the centre. The extremely primitive structure of the abdominal joint persisting

in Proscolia, suggests that Scoliidae descended from the most primitive Tiphiidae of the type of Anthoboscinae, if not from an even more primitive ancestral group. Mutillidae retained no such primitive characters (perhaps with the exception of the closely spaced basal hooklets on the posterior wing, but the primitive nature of this character is not obvious) and may have diverged, for example, from the same stem as the advanced Tiphiidae of the subfamilies Myziniinae, Tiphiinae and Brachycistidinae. The features in which Mutillidae are similar to the above groups, are the structure of their abdominal joint and the base of their mesacoxae tapering into a tube (the latter feature is less reliable because it appears independently in most Bradynobaenidae, excepting Apterogyninae, and in the group Sierolomorphidae, Falsiformicidae and Formicoidea); the structure of the last sternite in males is more primitive, which makes it impossible to derive Mutillidae from the direct ancestor of the three subfamilies of Tiphiidae mentioned earlier.

Thynninae that are on a somewhat lower morphological level, and Methochinae that are very close to Thynninae, particularly in the structure of their genitals, also have a number of characteristics in common with Mutillidae. Their females are wingless, but still display a relatively complete segmentation of the thorax. The tendency to form a tilted platform at the apex of the first metasomal sternite is here clearly pronounced; the posterior corners of the sternite tend to articulate with the corners of the second tergite, and a fossa tends to form around the joint of the scape with its radicle. These characters are clearly observable, for example, in Rhagigaster Guerin. Methochinae exhibit other features characteristic of Mutillidae: reduction of the lobules anteriorly of the mesocoxae on the one hand, and of the raised platform posteriorly of them on the other, and narrowing down of the base of these coxae into a tube. The features characteristic of many female representatives of Thynninae are, similarly to those of Mutillidae females, the thickening of the posterior margin of the seventh sternite and the frequent narrowing down of the opening for the ovipositor

(even though the latter is achieved here by way of changes in the shape of the major part of the sternite rather than by the adgrowth of the lobules). Taking all this into account, Mutillidae may be regarded as descendants of Tiphiidae that are close to Thynninae. Furthermore, it may be inferred that this family evolved not only as a result of the optimized abdominal articulation, but also because of the appearance of other morphological characters (such as the reduction of the sutures on the thorax in females, flattening of their thorax on the sides as a consequence of their digging activities becoming less intensive, narrowing of the opening at the apex of the abdomen in females, etc.), and first of all because of the changes in their biology (i.e. the developing on the larvae of Sphecoidea rather than on the larvae of beetles).

Brothers (1975) holds a different view regarding the phylogenetic relations of Mutillidae: he believes them to be close to Sapygidae and derives both families from a common ancestor with Tiphiidae. Sapygidae and Mutillidae are, indeed, biologically close, since both develop in nests of aculeate insects, mainly bees, but, judging from the biology of Fedtschenkiinae (Bohart, Shuster, 1972), Sapygidae attack primarily vespoids of the family Aumenidae. Mutillidae may secondarily change to completely new hosts, such as the puparia of dipterous insects, larvae of beetles or Lepidoptera, or even develop in the oothecas of cockroaches, probably on the larvae of Evaniidae (Mickel, 1974); their ability to get hold of active prey does not appear p.127
to become restored in such cases. However, the respective modifications in the structure of the last sternite in the females of Mutillidae and Sapygidae associated with their change-over to a relatively immobile kind of prey, are entirely different, as was mentioned earlier. The two families also exhibit a number of common features in their morphology, but their treatment by Brothers is far from being incontrovertible. The absence of a platform on the metathorax and the lack of lobules on the meso-thorax may differ in origin (being primary in Sapygidae, but secondary in Mutillidae, judging from the presence of their rudiments;

fig. 162i). According to Brothers, the frons above the antennae forms isolated tubercles (lobules) in Mutillidae and Sapygidae, whereas in Tiphiidae it is raised in the form of a transverse rib; in reality among Sapygidae the tubercles are characteristic only of Fedtschenkiinae (moreover, a virtually identical structure has been encountered in Tiphiidae, e.g. in the males of Pterombrus Sm.), while Sapyginae develop a typical costa. The small jugal region of the posterior wing separated by a deep incision has been encountered in many groups of Aculeata s.str. and can hardly be regarded as a reliable character, and the reduction of the free end of Cu in the posterior wings is not characteristic of all the forms of Mutillidae. It is lacking in the most primitive groups (in Myrmosinae, including Protomutilla Bischoff, and in Pseudophotopsidinae), but in many other Mutillidae the end of Cu is free, and there is really no need to attribute it to the evolutionary reversion (restoration of a previously reduced vein), as Brothers does it. The two primitive subfamilies also have a number of their own distinctive specializations, and the reduction of the terminal segment of Cu may prove to be one of them. The same may be said with an even greater justification regarding the presence of the metathoracic spiracle lost by Tiphiidae and Mutillidae, in the larvae of Sapygidae (i.e. of Sapyginae, since the larvae of Fedtschenkiinae are not known). The characters accounting for the similarity of Mutillidae and Sapygidae with regard to the structure of their genitals (the valves of the penis are joint in these insects by a membrane and only at the base) are shared to a certain extent by some forms of Tiphiidae (Meria F., Pterombrus Sm.), by many ants and by some bees which resemble them even more in this respect (e.g. Hylaeus F.). These characters therefore cannot be regarded as particularly reliable. As concerns the general structure of male genitals, Sapygidae resemble much more certain forms of Bradynobaenidae (particularly Typhoctes Aschm., where, in addition to other characters, the valves are also joint in a fairly mobile fashion and are not connected to the very top) than Mutillidae. The genitals of the latter display on the contrary a certain

resemblance to those of Thynninae and Methochinae (abbreviated bases of the volzellas* , a close connection between the penis and the commonly notched segment of the media margin of dorsal lobes of the gonocoxites).

Summing up the above discussion it may be stated that the features of similarity between Sapygidae and Mutillidae are considerably less convincing than their similarity in primitive characters to the whole assemblage Scoliidae+Tiphiidae+Mutillidae (first of all in the structure of the lower thoracic surface). Sapygidae may have branched off the main stem of Scolioidea even before the members of that assemblage diverged; moreover, the evolution of the family was accompanied first of all by changes in its trophic relations and by ensuing modifications in the shape of the last sternite in its females, as well as by the reduction of the stemming plates in their ovipositor and by certain other developments. It is fairly difficult to determine the time of the divergence of Sapygidae relative to that of Bradynobaenidae, another group that branched off early. The two families altered along different lines and at first glance Bradynobaenidae still closely resemble Mutillidae (in other features than Sapygidae), but Brothers has convincingly demonstrated that this resemblance is secondary. We have not succeeded in finding any reliable characters uniting either one of the two families with the three families mentioned earlier, or contrasting them all with some other family, and we are therefore compelled to leave this question open. We should refer to the most important morphological modifications involved in the evolution of Bradynobaenidae (their biology is unknown), the appearance of a roughly rectangular raised platform on the metathorax, the mesathorax pressed somewhat into the margin, the development of a secretion organ (the "felt-line") on the side of the second tergite of the metasoma which resembles superficially the felt-line of Mutillidae, but differs from it in details (Brothers, 1975); the displacement of the cross-vein cu-a more proximally to the bifurcation of M and Cu in the posterior wing (Brothers, 1975, believes this to be a primary condition, p.128

* Transliteration from Russian. Unable to find an English equivalent. Translator.

but the distinctly preferred distal position of cu-a among the Jurassic and Early Cretaceous Vespomorpha and the fact that it is wide-spread among the younger Aculeata testify to the opposite); the reduction of the wings and the characteristic modification of the thorax in females (see details in Brothers, 1975): and the appearance of paired stridulation fields on the metasoma.

The second "minor" stem of Scolioidea is represented by a mere two families Sierolomorphidae and Falsiformicidae that have been relatively little studied. If we restricted ourselves to examining their common characters, we would obtain essentially a primitive scolioid differing from the prototype of the superfamily mainly in the structure of the articulation of its basal metasomal segments that was described earlier (the optimization of the vertical and rotary motions). The reduction of venation is not however, characteristic of all the Falsiformicidae. Additional studies of Taimyrisphex Evans (fig. 179) from the Late Cretaceous of Taimyr (Santonian, Yantardakh), a form that was described as a probable representative of Sphecidae (Evans, 1973), and its comparison with the male specimen of Falsiformica A.Rasn. known from an incomplete remain found in the Cenomanian of Taimyr (Agapa), and with another representative of Falsiformicidae from Yantardakh that has not been described as yet, show that the first segment of the metasoma has been modified to a typical "formicoid" node only in female representatives of that family, but not in its males, and that Taimyrisphex, which has a fairly complete venation, also belongs to Falsiformicidae.

Since that node is often less strongly developed in male than in female ants, not only the presence of the node as such, but also the sexual dimorphism of Falsiformicidae with regard to that characteristic can be regarded as a character in which they are similar to Formicoidea. It is of course, far from obvious that the shape of the node has been inherited by the ants from Falsiformicidae, but there is no doubt that they display a similar tendency in that respect, which may be regarded as additional evidence in support of the theory that the ants, and with them the vespoids, descended from the same evolutionary

line within Scolioidea.

In concluding this chapter we shall present as usually the main data on the geological and geographic distribution of Scolioidea. Bradynobaenidae and Sapygidae are unknown in fossil state (there is an unconfirmed report of a find of Sapygidae in Baltic amber from the Eocene). In the recent fauna the former are restricted to the holarctic and neotropical regions, while the latter have a world-wide range. The distribution of Scoliidae is similar to that of Sapygidae except for the fact that the reports of their finds in the Oligocene and Miocene are unreliable, while that referring to the latter half of the Early Cretaceous is more reliable (see above). Tiphiidae and Mutillidae are also widely distributed at present, but the former have a reliable fossil record beginning with the Oligocene (Florissant in the USA and Svetlovodnaya in Primor'e) and are subject of less reliable reports since the Eocene (Baltic amber).

Mutillidae are undoubtedly present in Baltic amber and were identified, though with less confidence, from the Turonian in Siberia (Bol'shoi Kas). No Sierolomorphidae have been found in fossil state and in the recent fauna representatives of this family are known only from the holarctic region. On the other hand Falsiformicidae have not been found so far anywhere outside the Upper Cretaceous ambers from Taimyr.

The superfamilies Vespoidea and Formicoidea

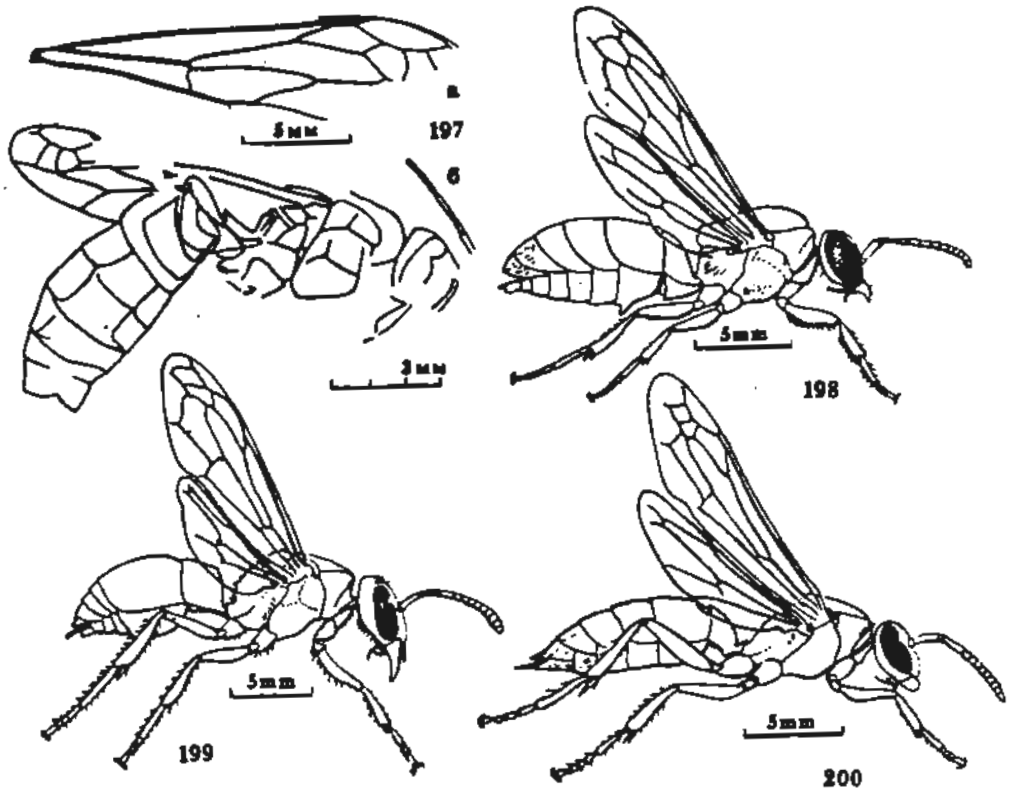
Wasps of the superfamily Vespoidea (figs. 197-200) and ants of the superfamily Formicoidea (figs. 201-209) have a number of common attributes and characteristic tendencies. In addition to the distinctive features characteristic of all the members of the vespoid group of superfamilies, both have geniculate antennae. Antennae of this kind are not developed in some of the more advanced Masaridae and in many male ants, including males of their primitive forms, such as Sphecomyrminae. Whereas in Masaridae the non-geniculate antennae are almost certainly secondary, the sexual dimorphism of ants with regard to

this character may well be primary. Markedly reduced post- p.129
spiracular sclerites intergrown with the mesopleura are also characteristic of both superfamilies, as well as of Falsiformicidae and some other Scolioidea (such as Mutillidae). Hind legs primarily with cleaning devices; moreover, the brush (strigilis) occupies practically the whole length of the spur. The articulation of the first metasomal segments is modified along the same lines as in Falsiformicidae and Sierolomorphidae (see figs. 178-180), but is complicated further by the articulation of the first sternite with the second tergite, as a result of which Vespoidea lost the ability to perform rotary motions at the joint. The sternite may have a prominent (convex) profile, which may easily prove to be a synapomorphism of the two superfamilies. There may also form a true tilted platform at the apex of the first sternite (in Polistes Latr, Dorylus F., fig. 162 1). That sternite may also have other shapes, as has been observed in some Masaridae (Masarina Rich., Celonites Latr.). Both groups have sharp lower corners of the pronotum that may be connected in a fixed manner to the mesopleura, but this feature has also been encountered in Scolioidea. The biology of the two superfamilies also has many features in common, their having abandoned the habit of supplying each individual larva with one single victim in particular, and the ensuing change to regularly carrying the prey into their nest and to the oviposition in an empty nest. These features are completely atypical of Scolioidea, at least of the forms of Scolioidea, the biology of which is more or less known, but it is premature to claim that the ants and social wasps are unique with regard to this characteristic (within the vespoid group of superfamilies) or that their similarity has been inherited, until the biology of Sierolomorphidae has been studied.

Some of the evolutionary tendencies that may be regarded as characteristic of the superfamilies discussed, are as follows: the fusion of the first tergite and sternite and the p.131
development of multidentate mandibles (which may be elongated) in advanced ants and wasps; the appearance of the long and pointed upper lateral corner of the pronotum resting on top of the tegulae in all the wasps and in Dorylinae among the ants (the latter are

also similar to the vespoids because the M+Cu bifurcation of their forewing is markedly displaced proximally); the loss of the jugal lobe in most of the ants and in many wasps (this is also characteristic of Sierolomorphidae, but is found rarely in the main group of Scolioidea and has been encountered only in advanced Mutillidae and in Eotillini among Bradynobaenidae); lastly, the sociality and direct feeding of larvae (Vespidae and all the ants).

Figs. 197-200



Representatives of the superfamily Vespoidea
197-Curiosivespa magma A.Rasn., Masaridae Euparagiinae; Upper Cretaceous from Southern Kazakhstan: a-Holotype; b-Specimen N° 2783/261 tentatively referred to this species; 198-Paragia sp., Masaridae Paragiinae; recent; 199-Abispa sp., Eumenidae; recent; 200-Polistes sp., Vespidae; recent; (197a-from Rasnitsyn, 1975a, 1975b-original drawing; the other drawings are from Riek, 1970b).

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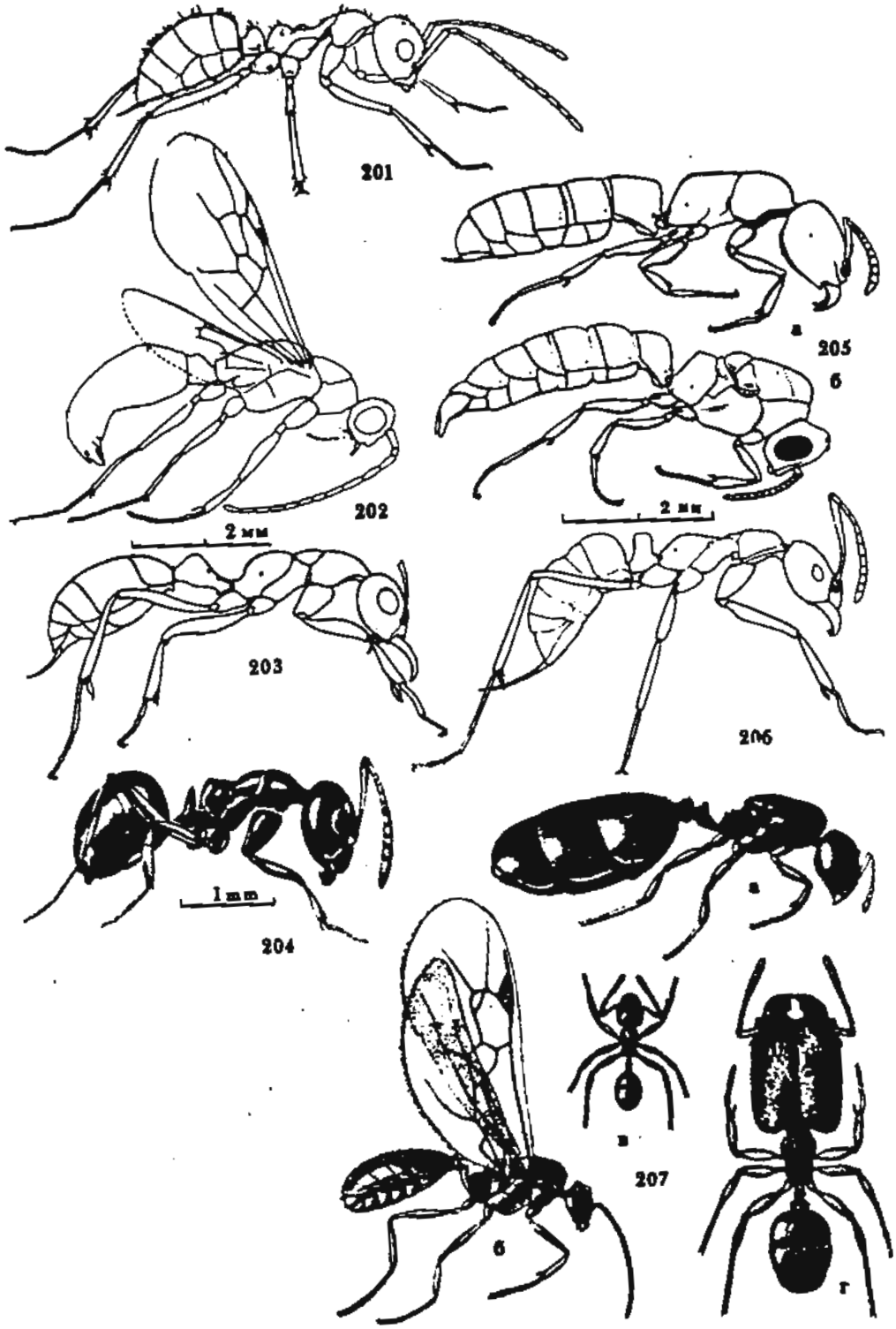
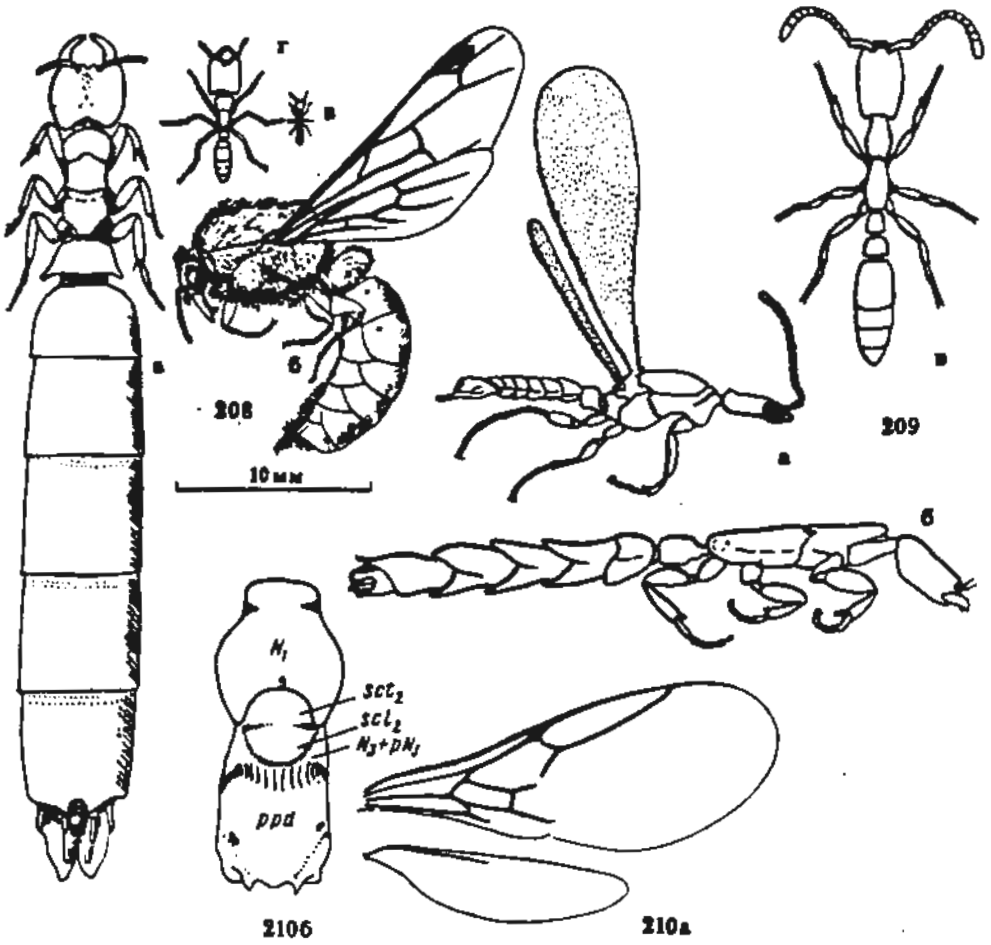
Figs. 201-207



Figs. 208-210



Figs. 201-209

Representatives of the superfamily Formicoidea

201-Sphecomyrma freyi Wilson et Brown, Formicidae Sphecomyrminae; worker, Upper Cretaceous, Canada; 202-Palaeomyrmex zherichini Dlussky, Formicidae Sphecomyrminae; male, Upper Cretaceous, Taimyr; 203-Methomyrmecia macrops Clark, Formicidae Myrmeciinae; worker; recent; 204-Prolasius sp., Formicidae Formicinae, recent; 205-Amblyopone pluto Gotwald et Lēvieaux, Myrmicidae Ponerinae: a-worker; b-male (wingless); recent; 206-Leptogenyc purpurea Emery, Myrmicidae Ponerinae, worker, recent; 207-Pheidole Kingi instabilis Emery, Myrmicidae Myrmicinae: a-female; b-male; c-worker; d-soldier; recent; 208-Dorylus helvolus L., Myrmicidae Dorylinae: a-female; b-male; c-worker; d-soldier; recent; 209-Leptanilla spp., Myrmicidae Leptanillinae: a-L. minuscula Sant, male; b-c---L. ravelierii Emery, female and worker (201-from Wilson,

Carpenter and Brown, 1967; 202-from Dlusskii, 1975; 203 and 206-209---from Wilson, 1971; 204-from Brown and Taylor, 1970; 205-from Gotwald and Lévieaux, 1972).

Fig. 210
Structural details of ants
a-Wing, Apomyrma stygia Brown, Gotwald and Lēvieaux; Myrmicidae Ponerinae; b-Thorax of a worker, Manica rubida (L.), Myrmicidae Myrmicinae (a-from Brown, Gotwald and Lēvieaux, 1970; b-original drawing).

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With regard to their primitive characteristics Vespoidea p.132
and Formicoidea are close mainly to Sierolomorphidae and Falsiformicidae among Scolioidea. These characters include very weakly developed protective devices on their tibiae (the armament), their flat metathorax (which is also characteristic of Sapygidae), the primitive structure of the sixth sternite in their females (described in greater detail earlier), the absence of individuals with a markedly elongated or sharply downcurved stinger, and the longitudinally divided gonocoxites in their males; mandibles with a sectorial edge that are not (primarily) turned out and are perpendicular to the plane of their movements rather than parallel to it (in the "major" group of Scolioidea a similar structure may apparently be observed only in Methochinae and in some Brachycistidinae, but in the latter it is definitely a secondary development; moreover, in Polistinae the mandibles bear a slightly slanted row of four teeth at the top, as is also the case in Chrysidoidea. If this character is primary, then Polistinae are more primitive in this regard than the other Aculeata s.str., but it is equally possible that their tetradentate mandibles are a secondary character. We should mention here, however, another primitive (relative to ants, Sierolomorphidae and Falsiformicidae) character persisting in Vespoidea, the broad base of their mesocoxae. We should also mention that the broad, gently curved mandibles

that are not turned out, are found only in the two superfamilies discussed among Aculeata s.str.

The characters described above combined with the modification of the first metasomal tergite in the females of Falsiformicidae to a structure analogous to the node found in ants, permit us to regard Vespoidea and Formicoidea as superfamilies that are close to one another and to the families of the "minor" branch of Scolioidea. At this time it is impossible to define their relationship more precisely (i.e. to determine whether the ants and Vespoidea diverged off Scolioidea as one single stem or separately), since our knowledge of Sierolomorphidea and Falsiformicidae is rather limited and the common specializations of the two superfamilies discussed either arise independently (the morphological features listed at the beginning of this part of our work) or are inaccessible for comparison with corresponding characters of Sierolomorphidae and Falsiformicidae (the characters of their biology). This also prevents us, of course, from elucidating the modifications involved in the formation of Vespoidea and Formicoidea. For the former we may indicate perhaps the hypertrophy of the posterior corners of the pronotum and the intergrowth of its lower corners with the mesothorax, as well as the reduction of the stemming plates in the stinger. The ability of Vespoidea to fold longitudinally their anterior wings, the stretched-out base of their 1m-cu cellule, and their reniform* eyes are often mentioned as their typical attributes but are not characteristic of many primitive Masaridae. In addition to the sociality and other biological attributes that are unknown among Sierolomorphidae and Falsiformicidae, the most prominent characters of ants are the dimorphism of their females (the existence of a wingless workers' caste) and the presence of metapleural glands which fulfill an antiseptic function and may also be genetically related to sociality (see Wilson, 1971). The presence of the node is a less significant diagnostic feature in ants: it is relatively weakly developed in many Amblyoponini and may be a primary condition.

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* Or gemmiform (the Russian word "pochka", from which the adjective used here is derived, means both a bud and a kidney). Translator.

We follow Richards (1962) in dividing Vespoidea into three families: Masaridae, Eumenidae and Vespidae. These families can be much more easily differentiated on the basis of biology rather than morphology, even though not all their biological differences are absolute (data from Wilson, 1971; Lin, Michener, 1972; Iwata, 1976). Sociality is a characteristic feature of Vespidae (but Stenogastrinae are often subsocial, i.e. the females of this subfamily rear their progeny in solitude; in other cases there may be several females in the same nest, which may include workers). In addition to preying on the larvae of insects (mainly Lepidoptera), Vespidae prey on imagos of different taxonomic groups (this can already be observed in Stenogastrinae, but does not appear to be characteristic of all the members of this family). Feeding is of the direct kind, with ingluvial food (may also be observed occasionally in Eumenidae); several (more than two) larvae are reared at the same time. The nest is made of "paper" (i.e. masticated wood); only some Stenogastrinae make clay nests (in the other families the nests made completely of "paper" are found in very exceptional cases and do not seem to be a stable characteristic even within individual species). The cells do not taper upwards; their openings are often (primarily?) oriented downwards, less often laterally, but never upwards. p.13

Eumenidae and Masaridae are solitary or subsocial. They commonly prey on larvae of insects (mainly those of Lepidoptera, less often of beetles, sometimes of sawflies, etc.), or (rarely) on spiders. Most Masaridae (excepting Euparagiinae which prey on weevil larvae) gather pollen and nectar. There are no known instances of attacks on insect imagos; cases of masticating the prey and feeding it directly are known for Eumenidae, but are extremely rare; simultaneous rearing of two (but no more than two) larvae has been observed, but is also extremely rare. The nests are commonly made of mud or clay, less often with the use of resin, chewed-up leaves, etc., but masticated wood is utilized extremely rarely; the available ready-made shelters are used often. Cells that are not tapered towards the exit and are

oriented downwards, appear to be unknown. Most Masaridae distinctly differ from Eumenidae (provisioning of the nest with pollen and nectar), but Euparagiinae preying on mining larvae of weevils, are similar in this character to some Eumenidae.

As concerns the morphological characters, they can be effectively used as criteria for differentiating subfamilies, but not families (Richards, 1962).

The three families of Vespoidea are widely distributed in the recent fauna; moreover, Masaridae, which are associated largely with arid regions, are not characteristic of the tropical regions. In fossil state this superfamily is known since the latter half of the Early Cretaceous (Barremian-Aptian? of Mongolia, Bon-Tsagan), where there have been found impressions of seemingly diversified Masaridae that are close to Euparagiinae, including those closely resembling Curiosivespa A.Rasn. from the Late Cretaceous (Turonian) of Kazakhstan (Kzyl-Zhar). Eumenidae and Vespidae are known only from the Cenozoic, the former since the Paleocene (Zerkal'naya in Primor'e) and the latter since the Eocene (Baltic amber and a number of other localities).

Ants (figs 201-209) are united within one single family Formicidae, but the morphological and biological differences between them are too great for this family to be comparable with other families of Hymenoptera. Modern notions of the phylogeny of ants suggest a way of differentiating this group. According to Brown (Brown, 1954; Wilson, Carpenter and Brown, 1967), there are two main phylogenetic stems of ants which he designates as the myrmecioid and poneroid assemblages. At the base of the former assemblage are Sphecomyrminae, from which Myrmeciinae and Aneuretinae (which were subsequently raised to the rank of a tribe within Dolichoderinae) originated. The primitive Myrmeciinae of the type of Nothomyrmecia Wheeler gave rise in their turn to the subfamily Pseudomyrmicinae. According to Brown, the position of Formicinae in this group is not entirely clear, but Eisner (1957) derives them together with Dolichoderinae as part of the same stem (including Aneuretini) on the basis of the structure of their proventriculus; furthermore, he believes that

Pseudomyrmicinae descended from the base of the stem which gave rise to Formicinae and Dolichoderinae rather than directly from Myrmeciinae.

Brown places Ponerinae (presumably the tribe Amblyoponini, which Eisner shows as a primitive, but distinctly separate group because of the specific structure of its proventriculus) at the base of the poneroid assemblage. Primitive Ponerinae gave rise to more advanced members of that subfamily, as well as to other subfamilies either directly (Cerapachyinae) or via advanced groups: Myrmicinae by way of the tribe Ectatommini, while Dorylinae* and Leptanillinae originated from some advanced Ponerinae, possibly as two to four independent roots. Eisner directly relates Dorylinae to Myrmicinae because of the reduced proventriculus in both groups. The position allocated in these systems to Dorylinae (together with Ecitoninae) and to Leptanillinae that are close to them, arouses some doubts. Dorylinae resemble p.134
Myrmicinae on account of their reduced proventriculus. This character may be a result of the parallel evolution and appears to be less significant than the characters uniting this group and Leptanillinae with primitive Ponerinae, particularly with Amblyoponinae. The characters referred to are as follows: 1) The structure of the thorax in males with a very long mesonotum and with a pronotum that is markedly constricted in the middle and is elongated on the sides; moreover, its lateral corners are stretched out behind the humeral nodes and pointed; among Amblyoponinae this type of thoracic structure may be found in the males of Apomyrma Brown, Gotwald et Lévieux; 2) Venation of the wings with the Imcu cellule expanded towards the base of the wing; the base of that cellule is located considerably more proximally than the cross vein cu-a (Dorylinae, fig. 208, Ecitoninae,

* The tribe Ecitonini was subsequently (Brown, 1973) separated from Dorylinae as a separate subfamily, which, judging from their position in the system accepted in that work, is, however, related to Dorylinae.

Apomyrma, fig. 210a, and, to a lesser extent, Typhlomyrmex Mayr among Amblyoponinae; in Leptanillinae the venation is reduced); 3) The metasoma without the constriction between the second and third segments in male and female individuals, and in Dorylus F. and Cheliomyrmex Mayr also in workers; the constriction may also be lacking in primitive Ponerinae, and Apomyrma shows signs of sex dimorphism in this character; 4) The nomadism characteristic of the subfamilies listed above, has also been observed in some Ponerinae; moreover, the greatest resemblance in this respect has been observed in the representative of Amblyoponinae (Onychomyrmex Emery; Taylor, 1972). It is therefore more probable that Dorylinae, Leptanillinae and Ecitoninae diverged early off Ponerinae forms similar to Amblyoponini.

The derivation of Myrmicinae from advanced Ponerinae of the tribe Ectatommini is equally questionable. The mesonotum in workers of many Myrmicinae retains the normal aspect, with a discrete scutellum, characteristic of winged castes to a considerably greater degree than the mesonotum in workers of Sphecomyrminae, let alone of Ponerinae, be they the most primitive ones. This structure of the mesonotum is particularly clearly observable in primitive Myrmicinae, especially in Manica rubida atr. (fig. 210b).

The differentiation of ants with the use of the two assemblages instituted by Brown [the myrmecioid (Formicidae s.str.) and the poneroid (Myrmicidae) assemblages] therefore appears to be the easiest and most obvious way of dividing them into families. Because of the morphological and, to a lesser degree, biological segregation of Dorylinae+Ecitoninae+Leptanillinae from the other Myrmicidae, it is tempting to divide ants into three rather than two families, but to do so we must prove that "Dorylidae" is a monophyletic family. As long as it has not been proven it is wiser to restrict ourselves to the institution of Myrmicidae and Formicidae. For the time being the only character that can be used as their formal diagnostic feature is the difference in the structure of their proventriculus: in Formicidae the proventriculus is sharply constricted at the base and is separated from the mid-gut by a slender and relatively long tubular

segment, whereas in Myrmicidae it narrows down gradually and the slender tubular (cylindrical) segment anteriorly of the mid-gut is barely observable; this is also the case in the forms where the proventriculus has been reduced (Eisner, 1957).

Another character evidencing that the two families are separate units is the formation of the petiole characteristic of ants (i.e. the constriction sharply separating the first metasomal segment from the other segments). Judging from Amblyopone (fig. 205), in Myrmicidae the tergite initially remained quite normal and the separation occurred through the constriction of the base of the second segment, which subsequently spread to the apex of the first segment; a fairly similar structure also persists in the males of Leptanillinae (fig. 209). In Formicidae (in Sphecomyrminae, particularly in Palaeomyrmex Dlussky, fig. 202) there was initially no constriction at all and the petiole formed as a result of the appearance of a node on the exterior of the first tergite, as is the case in the females of Falsiformica (Fig. 180). In many Myrmicidae (in Dorylinae, Ecitoninae, Leptanillinae and in many Ponerinae) the petiole is, indeed, similar in shape to a normal segment, which does not seem to be the case in Formicidae.

The oldest ants are known from the Late Cretaceous (Turonian) of Kazakhstan, where we identified representatives of both families, i.e. several genera of Ponerinae and a genus of an indeterminate position belonging either to Specomyrminae or to Dolichoderinae (Dlusskii, 1975). The only forms identified in the younger Early Cretaceous resins are Sphecomyrminae (Santonian in the USA, Magothy; Wilson, Carpenter and Brown, 1967; Santonain in Taimyr, Yantardakh; Dlusskii, 1975; Campanian in Canada; Carpenter, personal communication). The first Dolichoderinae identified as such with complete confidence appear in the Paleocene (Zerkal'naya in Primor'e), and in the Eocene we already find representatives of all the subfamilies other than Leptanillinae and Ecitoninae (the only report available regarding a find of Dorylinae in Baltic amber needs to be confirmed); moreover, Formicinae and Dolichoderinae predominate among them. Beginning

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with the Neogene the latter give way to Myrmicinae; Brown (1973) points out that this succession of the dominant forms occurred after the beginning of the Neogene, in the course of the Miocene, but he uses data on the age of the deposits at Florissant that are out of date; in reality these deposits are of the Oligocene age. Both families have a global range in the modern fauna. The subfamilies having a world-wide range are Formicinae, Myrmicinae, Ponerinae and Pseudomyrmicinae (the two latter subfamilies are rare in the temperate zone of the holarctic realm); Myrmicinae are confined to Australia, although in the past they existed in South America (Upper Oligocene or Lower Miocene of Argentina, Pilcaniyeu) and in Europe (Eocene, Baltic amber); Ecitoninae - to the New World, Dorylinae and Leptanillinae - to the Old World, but even here they practically never penetrate into the regions with a temperate climate, and Leptanillinae are unknown in the Ethiopian realm.

The origin of sociality among ants

Ants are far from being the only group of social aculeate insects. This superfamily is unique and merits a special attention primarily because sociality is characteristic of all its members and has consequently been raised to the level of phylogenetic analysis accepted in this work. Furthermore, the manner and the ways in which sociality arose and evolved among ants are not as clear as those of other insects.

We must define first of all the concept of sociality. If treated within the general framework of biology, it is a highly complicated question, but in entomology the problem is relatively simple; the insects referred to as social are those, among which some individuals are regularly occupied with rearing the offspring hatched from the eggs laid by other individuals. There is a more precise and more minutely differentiated classification of insects with respect to the degree of their sociality (Wilson, 1971; Lin, Michener, 1972), but at the moment there is no need to resort to it.

The most readily understandable reasons for the development of social life can be found among termites, which must remain in constant contact to exchange intestinal symbionts and for the purposes of defence against their enemies (Wilson, 1971; Lin, Michener, 1972). The main contributing factor to the realization of sociality among termites is their incomplete metamorphosis or rather their attributes causatively related to it and favouring the development of sociality. These attributes are as follows: 1) The mode of existence of their nymphs similar to that of their imagos, which permits the nymphs to act as workers. The advantages offered by the nymphs in this plan are their natural inability to reproduce and the fact that their utilization makes it possible to dispense with the difficulties involved in reducing the number of males, which would otherwise be necessary. Wherever it is impossible to employ preimaginal stages (as is the case with Hymenoptera), the role of the workers can be undertaken only by females, since they are the individuals involved in the nesting activities (construction of the nests and rearing of the progeny). Arbitrary (by the choice of the female) sex determination is impossible among termites and among most of the other insects. Therefore an increase in the number of their females would be accompanied automatically by the production of excessively large numbers of males which perform no useful function in the nest. The utilization of nymphs in the role of workers permits them to avoid this complication. Of course, this solution has also unfavourable consequences: the limited duration of the nymphal stage and its subsequent change to an imago leads to a continuous emergence of "superfluous" imagos. But these consequences can be readily blocked by delaying the metamorphosis, which may be accomplished, for example, by maintaining a high production of the juvenile hormone. 2) Incomplete metamorphosis eliminates the period of the pupal rest, which in insects, such as Hymenoptera, p.13 interrupts, as a rule, the contact between the female and its offspring, except for the cases, when the pupae are not isolated either by cocoons, or by individual cells, which practically never happens among the solitary and socially primitive Aculeata

s.str., i.e. in the only social group of Hymenoptera. Of course, a forced break in the interaction of the mother with its offspring is not an insurmountable obstacle and does not preclude the restoration of the contact between them upon the attainment of the imaginal stage by the young, but it appears to happen very rarely (e.g. in Cerceris rubida Jur.) among the insects with a solitary mode of life (Grandi, 1961; quoted after Wilson, 1971).

The paradoxical case of "social aphids" awaits a detailed study. According to Aoki (1977a and b) in some aphids the first-instar larvae are dimorphous with one of the forms fulfilling the functions of the soliders' caste.

Prior to proceeding with our discussion of aculeata insects we must separate the causes and conditions leading to the development of social behaviour. The causes comprise the factors inducing (stimulating) the transition to sociality, i.e. the factors increasing the acceptability of the co-operation among the individuals and of the division of labour in rearing their offspring. By conditions we refer to the factors facilitating or at least not hindering this transition.

At first glance the most obvious cause of sociality is the increase in productivity implicitly resulting from the division of labour. It does not explain, however, the first stage of evolution, i.e. the change-over to the communal nesting prior to the advent of the division of labour. We must look here for other explanations. Such explanations have been offered, in particular, by Wilson (1971) and Lin, Michener (1972). According to these authors an important factor is the defence of the nest against parasites and commensals. This is particularly important for Aculeata, the nests of which are arranged in clusters and have clearly observable entrances. Another important factor is the acceleration of the process of construction and provisioning of the nest which makes it possible to reduce the length of time required to produce a generation, and to increase the number of generations per unit of time. This is naturally most effective in the event of a lengthy reproductive season, which compels us

to associate the origin of social aculeate insects with a warm climate*.

The authors quoted above also attribute a great deal of importance to the so-called "Hamilton's effect", i.e. the by-effect of the haplodiploid sex determination, on account of which the genetic similarity between the sisters is greater than that between each sister and its respective daughters. More precisely, in the simplest case two sisters have an average of 3/4 common genes, while a mother and its daughter have only 1/2 of their genes in common (if the genotype of the female for the given locus is ab and that of the male is c, then half the daughters will have the genotype bc and the other half ac. The mother will have only one of its two alleles identical to an allele in each of its daughters, while half of its daughters will also be identical in one of the alleles, and the other half in both). Let us assume that a female joins its mother and, assisting it with nesting, increases the progeny of the mother (i.e. the number of its own sisters) by the same number that it could have reared on its own. By doing so it ensures the reproduction of its own genes (or, rather, of genes identical to its own), hence its input into the gene pool of the next generation, 1 1/2 times more effectively than by rearing its own offspring. Under these circumstances selection will naturally be directed against independent nesting of young females, but will favour their co-operation with the mother.

A less drastic variant of Hamilton's effect is the case of a female joining its sister rather than its mother and contributing thereby to the increase in the number of its nieces (and

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* It is, indeed, correct in the case of ants; they appeared during the Cretaceous, not earlier than in the Neocomian and not later than in the middle of the Cretaceous period (Albian-Cenomanian), where there were no regions on the territory of Eurasia with significant fluctuations in the mean monthly temperatures. Sinitsyn (1966) distinguishes there only two thermal types of climate, tropical and boreal, with the average monthly temperature intervals of +28+25° and +18+15°, respectively. Under these circumstances there can be no question of a limited reproductive season.

nephews). In the event of both sexes being diploid, its genetic resemblance to its nieces will be equal to 1/4, whereas here it is 3/8, i.e. 1 1/2 times greater once again. Admittedly, its resemblance to its daughters is even greater (1/2 of common genes). Therefore in this case Hamilton's effect ceases being a cause of the development of sociality and becomes instead a favourable condition (as compared to the insects devoid of the haploid sex determination; see also Wilson, 1971, p.333). p.137

Among the probable causes of the development of sociality among the aculeate insects we may thus list the ability to protect the nest, the acceleration of its construction and provisioning, and Hamilton's effect.

The first factor comes into effect in the event of the nest being in danger of infestation by parasites through the open entrance (or in the case of the refusal to seal the nest in spite of the presence of parasites) on account of the aggregation of a number of females within the same nest thus providing for a more effective defence thereof. This presupposes first of all a lengthy provisioning of the nest (mass supply of the cells or, in the event of provisioning in one single operation, a multicellular nest) and, secondly, a nest with an open and readily accessible entrance, particularly in the case of the nests concentrating in groups,which is a particularly attractive situation from the viewpoint of parasites.

It would appear that the only preconditions for the development of sociality under the effect of selection for a speedier construction and provisioning of the nest are a lengthy nesting period and an indefinite number of generations. However, in addition to that it presupposes, like any other selection, the existence of functions that can be divided among the affiliated females (at least carrying the prey to the nest in addition to the oviposition). The mere building of the nest is not enough, since in the absence of repeated deliveries of the prey into the nest there is no need for continuous construction activities.

Lastly, the prerequisites for realizing the advantage of Hamilton's effect are a) repeated provisioning of the nest (mass provisioning or, in the case of a single-operation provisioning, the development of a large number of larvae in the same nest); otherwise it would be difficult to imagine what kind of assistance young females could give their mother in rearing their sisters; and b) formation of a matrifilial colony, i.e. the affiliation of young females with their mother. Until these conditions are met, Hamilton's effect remains inactive and the stages preceding the formation of a matrifilial colony must be realized under the impact of other factors.

The two factors commonly regarded as prerequisites for the development of an eusocial (matrifilial) colony are progressive provisioning of the nest by solitary wasps and bees, and colonial parasitism. Progressive provisioning with the mother regularly checking up on the situation in the cell and supplying the larvae with food whenever it is necessary, does, indeed, ensure a lengthy contact of the female with its offspring and enables it to rear several larvae simultaneously. In reality the importance of progressive provisioning is, however, greatly exaggerated. This type of provisioning is wide-spread among Specidae, but in spite of the behavioural, morphological and taxonomic diversity of that group, we know one single case of sociality among them (Microstigmus comes Krombein; Matthews, 1968). In spite of the presence in that genus of species with progressive provisioning, M. comes itself practices mass provisioning (Richards, 1972), similarly to fossorial wasps with a less well-developed sociality (several of their females aggregate within the same nest and may even practice division of labour, but each rears its own offspring; for more details see Miller, Kurczewski, 1973; and Peters, 1973). Mass provisioning also appears to be characteristic of most of the bees evolving towards a social life, and may even persist in highly social forms, such as Meliponini (Michener, 1974; Wilson, 1971). It would appear that sociality evolved against the background of progressive provisioning only in bees of the tribe Ceratinini and in Vespidae.

This suggests that progressive provisioning should not be included among the major conditions for the development of social life. Progressive provisioning is commonly regarded as a prerequisite for the evolution of sociality of the type of a matrifilial colony (affiliation of daughters with their mother), but seeing the case of Cerceris rubida (see above), it may be premature to extend the conclusion drawn earlier to this particular trend in the development of sociality. There are very few incontroversial examples, where sociality evolved via the matrifilial colony, that are known to us (according to Lin and Michener, 1972, there is only one case of this kind, i.e. the "allodapine bees" from Ceratinini, but Wilson maintains, 1971, that even this case may be debatable). Unlike Lin and Michener (1972), Wilson (1971) believes that Vespidae also underwent the stage of the eusocial colony, while Evans and West Eberhard (1970) are generally disinclined to regard the matrifilial colony as a significant factor in the evolution of sociality. Fouding of the nest by several females, for the most part by sisters (see the works referred to), is a wide-spread phenomenon and makes it difficult to agree with the views expressed by these authors. p.138

The evolution of sociality via the colony of sisters (i.e. the sororious colony) appears to be better documented than the case of the matrifilial colony (Zucchi, Sakagami, de Camargo, 1969; and Succhi, Jamane, Sakagami, 1976; the latter work is particularly interesting in that it demonstrates that females of the same generation may affiliate even if the nest is provisioned progressively). Nevertheless Wilson's general conclusion appears to be the most valid one. The author believes that sociality evolved along both lines and that it is not always possible to draw the boundary between them. Be it as it may, the matrifilial way is certainly no more wide-spread than the pattern of sororious colonies. This is very odd, since Hamilton's effect should favour the development of the eusocial colony. It could be argued that the matrifilial colony is at a disadvantage because social organization evolves there only in the second generation, whereas in a colony of sisters it arises already in the first generation (Lin, Michener, 1972), but this is contradicted by the strictly matrifilial (often

probably secondary) pattern of colony foundation among many highly social Hymenoptera (particularly in the temperate zone). It would appear that the losses of adaptability caused by the delay in the realization of sociality, are not particularly great in the case of an eusocial colony. Perhaps the main reason is the existence of the pupal period interrupting the contact between the successive generations and making it difficult for the matrifilial colony to become established, but so far there are too few data to assess the importance of this factor.

It was Malyshev (1966 and his earlier works listed in the bibliography) who drew our attention to colonial parasitism as a precursor of sociality by his hypothesis of the origin of ants. Malyshev's postulate regarding the taxonomic position of the ancestors of ants (Bethylidae of the genus Scleroderma (Latr.!) is, of course, unacceptable (ants have generally no relation to Chrysidoidea, particularly to their highly specialized representatives, such as the genus referred to). However, even if we leave this point aside, it is doubtful that colonial parasitism presupposing development of several generations of the parasite on the same victim, can evolve into a social mode of life, despite the obviously close contact between the different generations (to the point of mating of the mother with its male offspring) and a certain division of functions. The distribution of functions occurs here on the same principle as, for example, among the aphids (fully developed migrant females and underdeveloped females ensuring the highest possible rate of reproduction on an abundant source of food) and is totally unlike the division of labour characteristic of social insects. This is logical, since the functions differentiating the individuals in the latter case, are either lacking (preying, carrying the prey, and construction activities) or are barely developed among colonial parasites subsequent to the foundation of their colony. Infertile workers are of no use in the event of colonial parasitism, and selection will not favour their appearance.

We can now formulate the main factors which served as the causes or conditions in the evolution of sociality among Sphecoidea and Vespoidea. Its causes were the efficiency (adaptive value) of co-operation among the females in their defence of the nest (decreased mortality of the progeny), in their preying and building activities (reduction in the duration of a generation), and, in the case of a matrifilial colony, also the full impact of Hamilton's effect (the adaptive advantage of the increase in the number of female siblings relative to that of female offspring). The factors which acted as conditions making the transition to sociality possible, were: 1) The existence of readily divisible functions distributed in such a manner that the reproductive function as such was inhibited in a portion of the individuals (the continuous construction and preying activities, i.e. the repeated mass provisioning or the progressive provisioning, often also a compound nest containing several offspring at all times 2) Arbitrary sex determination; 3) If the first cause of sociality predominates (defence of the nest), colonial nesting; 4) In the event of a sororious colony - weakening of Hamilton's effect (the relatively small negative adaptive advantage of the increase in the number of nieces relative to that of daughters). p.139

Another important factor is the varying efficiency of the females with regard to the nest functions; given the right scale of variations, they may serve as a favourable condition or even as a cause of the co-operation and division of functions. These differences are quite real (see Lin, Michener, 1972, regarding Aculeata, and Dowell, 1976, regarding the parasitic Hymenoptera).

Detailed analyses of the concrete ways in which sociality arose and evolved under the effect of these factors (including aspects that have not been touched upon in our work) can be found in other works (first of all in those by Michener, 1974; Evans, West Eberhard, 1970; Wilson, 1971; and Lin, Michener, 1972; as well as in the literature listed in the bibliographies to these works).

So far we focused largely on wasps and bees; in the case of ants the situation is considerably more complicated, since they have not preserved either solitary stages, or stages intermediate between them and the true sociality. The biology of living ants offers no clues to their primary trophic specialization. Many of the primitive ants from the tribe Amblyoponini are specialized for Myriopoda that are geophilomorphic, but preying for them is much too unusual among aculeate insects to be able to regard Myriopoda as the primary type of prey without additional evidence to that effect; other ants are either polyphagous or exhibit a distinctly secondary trophic specialization. It is equally unclear whether their initial pattern of provisioning was of the single-action, progressive or mass type. Some of the distinctive attributes of ants, such as the absence of individual cells (the offspring being always kept in common chambers) and tending of the offspring (licking them, moving them around in the nest, etc.) have no clear-cut analogues among any of the other Aculeata s.str., and it is not easy to decipher the pathways along which they evolved. However, the main problem is that it is far from obvious whether the ancestors of ants met some of the causes and conditions prerequisite for the development of sociality. As is obvious from the further account, the attempts to reconstruct the evolution of sociality in this group yield therefore rather inconclusive results.

In order to visualize more clearly the hiatus between the mode of life of solitary wasps and that of ants, we shall first of all sum up the most pertinent biological characters of Myrmeciinae and Amblyoponinae, the most primitive ants in this respect (on the basis of data from Haskins, Haskins, 1951; Haskins, Whelden, 1954; Brown, 1960; Brown, Gothwald, Levieux, 1970; Wilson, 1971; and Gothwald, Levieux, 1972). In both groups the female is fertilized after it emerges from the parental nest and settles down in a cell built in the soil (commonly underneath a rock, tree trunk, etc.) or in decayed wood. The female of Myrmeciinae builds the cell itself, but among Amblyoponinae even mature colonies may apparently inhabit natural cavities (sometimes a cavity with tunnels branching off it, which may be

simply canals from dead roots); we believe this to be a more primitive state. Among Myrmeciinae the nests are founded by solitary young females; among Amblyoponinae they may be founded by several females. This suggests that the ant colony arose originally as a sororious colony. Furthermore, their young females may join the colonies already in existence. Among A. (Stigmatomma) pallipes Hald. this seems to be the rule rather than an exception, and new colonies arise by way of division. Females of Amblyopone may begin nesting (which includes preying, oviposition and rearing of the larvae) without fertilization. The nest founded by them is of the so-called partly closed type: the female leaves the nest in search of food (those of Myrmecia regularly forage for nectar and prey on insects only in the presence of larvae, but not of eggs or cocoons; those of Amblyopone, which are obligate zoophages, leave the nest less often, but regardless of presence or absence of progeny or the stage of its development). Furthermore, the foraging activities of the female continue even after the workers have been hatched (among Amblyoponinae they continue for a long time, among Myrmeciinae for a short period of time). The behaviour of Amblyoponinae was probably of a more primitive type, except for the loss of feeding on carbohydrates, but the extremely great (daily!) need of nectar in Myrmeciinae can also scarcely be a primary characteristic. Myrmeciinae lay eggs singly, Amblyoponinae lay them in packets, in common with most ants (a secondary state). Myrmeciinae prey above the ground and are commonly polyphagous, while Amblyoponinae are exclusively subterranean hunters in habit and are polyphagous or (more often) oligophagous (preying on geophilomorphic myriapods; the problem of whether the hypogeaic or the above-ground foraging is primary is discussed farther on). Amblyoponinae often do not dismember their prey and may not even kill it, but merely paralyse it and drag it closer to their larvae instead of feeding them individually. The larvae reach the prey on their own and commonly feed through the openings in its covering tissues made by the workers which fed on it previously, but they may also gnaw through its covers themselves thus exhibiting a much more primitive behaviour than that of Myrmeciinae, which dismember their prey and

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feed their larvae individually. Another wide-spread practice among Amblyoponinae is to drag the larvae to a large prey. Malyshev (1966) regards this practice as evidence of a genetic link with colonial parasitism. Wilson (1971) believes, however, that this type of behaviour could not have been primary, at least not for myrmecioid ants (i.e. for Formicidae s.str.). He therefore admits the possibility of the diphyletic occurrence of sociality in ants. What we said earlier regarding the relation of colonial parasitism to sociality permits us to regard this hypothesis as superfluous and to treat the conveyance of the larvae to the prey as a lateral evolutionary off-shoot, probably a blind alley, in the behaviour of ants. Furthermore, the workers of both groups commonly hunt and transport their prey singly. The exchange of ingluvial food among the adult individuals and among the adults and the larvae is developed considerably more in Myrmeciinae than in Amblyoponinae, among which the latter variant has not been recorded at all. On the other hand Myrmeciinae are more primitive in the sense that their females do not consume a portion of their eggs and larvae even in the case of an extreme shortage of food, whereas among Amblyoponinae this habit (a habit characteristic of ants) is already developed. Myrmeciinae, at least some of them, display another feature characteristic of ants: the modification of the wing muscles in fertilized females to a fatty body (food reserve). Amblyoponinae have not been studied in this respect. Imagos of Amblyoponinae emerge from the cocoon on their own, unlike those of Myrmeciinae and other ants, where emergence from the cocoon is impossible without the help of adult individuals.

It may thus be seen that primitive ants retain many attributes characteristic of solitary wasps and, in particular, of Scolioidea: mixed imaginal feeding on nectar and animal food (it is also widely developed among Scolioidea, but appears to be most common in Thynninae; Clausen, 1962), solitary subterranean preying and paralysing of the prey (even by the female after the appearance of the workers), imperfect construction (nests composed of one single very primitive chamber), a high degree of

independence of the larvae and of the emerging imagos (the absence of individual feeding and the independent emergence of the imago from the cocoon).

Among the characters distinguishing ants from their presumed ancestors, the features that may have some bearing on the development of sociality are as follows: 1. The co-existence in the nest and the fulfilment of the functions associated with reproduction by several adult individuals differentiated morphologically (primarily winged, but readily dealating females with a normally segmented thorax, and wingless workers with a reduced segmentation of the thorax, that are also females genetically speaking), as well as functionally (the females fulfil primarily the same functions as the workers, but whereas in the females the function of oviposition is hypertrophied to a greater or lesser degree, in the workers it is inhibited; moreover, the workers normally remain unfertilized). 2. The constant presence (excepting the time spent in foraging) of adult individuals in the nest. 3. Transportation of the prey to the cell prepared in advance (including the prey destined for feeding the imago). 4. Oviposition in the empty cell. 5. Development of the offspring in one single cell. 6. The absence of an individual food store for each larva. 7. The modification of the trophic specialization; the nature of this change remains unclear; it is only obvious p.141 that the diet of the larvae alters, since ants specialized, similarly to Scolioidea, for feeding on larvae of beetles leading a sheltered existence, are unknown. 8. The constant tending of the progeny (keeping the chamber clean, licking and moving around the offspring). 9. Succeeding generations of workers join the matrifilial nest and proceed with the nesting activities without mating. This may also be observed among normal females. 10. Trophallaxis, be it even weakly pronounced, appears to be a common feature among adult individuals (its presence in all the primitive ants has not been proven). 11. The appearance of metapleural glands, the secretion of which is responsible to the antiseptic environment in the nest.

Furthermore, it is possible that in all the ants, even in the most primitive ones, the wing muscles of females, unlike those of Scolioidea, alter after the fertilization to a fatty body acting as a food resource. Admittedly, this body does not seem to be particularly necessary, since the progeny is not fed on ingluvial food and the female hunts regularly, and further studies may show that some forms, such as Amblyoponinae, are incapable of forming that body.

The characters listed above allow us to reconstruct some of the circumstances under which sociality of ants arose and evolved. First of all the absence of wings in the workers evidences that the morphological differentiation of the primitive colonies occurred under conditions of hypogeaic preying. Otherwise, given the absence of individual cells and individual food stores, which appear to be the main factors responsible for the conservative choice of the prey, the above-ground transportation of the prey would have almost inevitably altered to its transportation by air. This change-over requires only a decrease in the weight of the prey to the level somewhat below the weight of the wasp itself (which is readily feasible in the event of repeated provisioning of the nest) and offers great advantages with regard to the speed of the delivery of food and to the size of the hunting area. It is not accidental that in the wasps which do not practice subterranean transportation, reduction of the wings is observed extremely rarely (Malyshev, 1966). It may therefore be inferred that the subterranean transportation is primary in Amblyoponinae. The fairly profound specialization of Amblyoponinae for the hypogeaic existence (their markedly reduced eyes and short legs) can hardly testify against the subterranean transportation of the prey being primary in the ants. The specialization of Amblyoponinae is determined not only by this factor, but also by their complete rejection of nectarophagy, which, judging from Myrmeciinae, could scarcely have occurred in the primitive ants. Moreover, their regular prowling above the ground in search of sources of carbohydrates should have been enough to prevent this kind of specialization.

The imperfect construction skills of Amblyoponinae, their hunting for relatively large prey, as well as the absence in the nests of the ants of any traces of individual cells or individual food reserves for their larvae also suggests that in the course of their evolution the ants may have bypassed the stage of mass provisioning and, unlike the other aculeates, changed directly from the single-action to the progressive provisioning.

The single-action pattern of provisioning rules out dragging of heavy prey for long distances through subterranean passages. The initial stages in the development of sociality among the ancestors of ants must therefore have occurred under conditions of a great population density of both these insects and their prey. These concentrations of prey were probably of a local and temporary nature, but they existed long enough to allow several successive generations of wasps to develop. Under these conditions there could easily arise dense populations of wasps that were often very similar genetically because their particular concentration evolved from solitary beginners with subsequent inbreeding (whereas Hymenoptera, as was mentioned earlier, are immune to inbreeding because of their distinctive genetics). In these circumstances and given the practice (be it even weakly developed) of transporting the prey, the nests may have been built right next to one another; moreover, they may not have been fully isolated on account of the imperfect construction skills of the ancestors of wasps. If the females readily made their nests in natural cavities in the substratum, the presence of several females and their prey in the same chamber must have been a frequent occurrence. Given the probable level of genetic p.142
similarity between the females (a prerequisite for the realization of the partial Hamilton's effect in the event of the formation of a sororious colony), variations in their ages and quality with regard to the nesting activities (examples of which among wasps and bees are cited by Michener, 1974, and Lin, Michener, 1972), it may be surmised that selection favoured communal nesting of the females and co-ordination of their activities. This

co-ordination may have led on the one hand to the replacement of the rigid "one female-one egg" relationship by a pattern under which the prey was supplied whenever it was needed (the transition to the non-individualized progressive provisioning), and on the other hand to the development of sociality via the sororious colony.

If we assume that throughout the successive reproductive cycles the female transports its prey to the same place (which appears most probable in the event of its using natural cavities in the substratum, particularly if these cavities are in the immediate vicinity to concentrations of the prey), then the conditions will prove favourable once again for the change-over to progressive provisioning and for the formation of the sororious colony in the next generation (because of the tendency of many Aculeata to return to the parental nest). If, however, we assume that the nesting cycles were lengthy, protracted, then the young females may find in the nest, upon hatching, their mother and the larvae, i.e. their sisters and brothers needing care and food. Assuming further that the ancestors of ants were capable, similarly to some Amblyoponinae, to proceed with the nesting activities without the fertilization and additional feeding on carbohydrates, it will be obvious that sociality may have easily evolved further on account of Hamilton's effect in its full form (through the matrifilial colony).

Indeed, under these conditions the young females should immediately start looking after the progeny present in the nest, to hunt, etc., but their oviposition will be blocked to a greater or lesser degree by their virginity, as well as by the competition of their mother, an old female reproducing for a long time. As a result of this the young females become workers, initially perhaps on a temporary basis, but changing later on to independent nesting (as in the case of social wasps of the genus Belonogaster Sauss described by Wilson, 1971) and thereupon on a permanent basis. The same processes leading to the appearance of workers may take place when the communities arise by way of the sororious colony. Regardless of the manner in which they evolve, the

result will be essentially the same: the development of true sociality and the appearance of ants. We feel that changes of the kind of morphological differences between the females and workers, trophallaxis, etc. should be referred to the further evolution of ants rather than to the processes resulting in their appearance, and are therefore outside the scope of this work.

In concluding our analysis of the phylogenesis of Hymenoptera we wish to refer once again to the chart of phylogenetic relationships of the superfamilies and families belonging to that order (see fig. 38). With respect to the lower Hymenoptera this scheme is close to the theories postulated by Ross (1937) and, particularly, by Benson (1938, 1951, 1952 and 1958), except, of course, for the position of Orussoidea and for the conclusion regarding the ancestral nature of Xyelidae relative to all the other Hymenoptera. The proposed scheme differs radically from the postulates of Königsmann (1977). The views held by the author on the subject of phylogeny of the higher Hymenoptera differ significantly from the traditional theories (Evans, West Eberhard (1970, fig. 14), and on the subject of Aculeata the position of the author is intermediate between the traditional (Evans, West Eberhard, 1970) and radical (Brothers, 1975) views.

PART IV

THE SUCCESSION OF HYMENOPTERAN FAUNAE

Chapter 1
Triassic and Jurassic faunae
Triassic period

The paleontological history of Hymenoptera* begins in the latter half of the Triassic period, when on the territory of the present-day Central Asia (Dzhyailoucho, Middle or Upper Triassic) there existed a distinctive ancient fauna of these insects. There have been found here various representatives of Xyelidae Archexyelinae (24 species, 11 genera), a subfamily close to the ancestral forms of all the other Hymenoptera, and a remain of Madygellinae, a more advanced subfamily. It should be noted that our assessment of the taxonomic diversity of Xyelidae on the basis of the material collected at Dzhyailoucho, may be far from realistic. The impressions obtained are markedly distorted because of the deformation of the enclosing rocks, and the system proposed for Archexyelinae has therefore been worked out very tentatively (see more details in Rasnitsyn, 1969, pp.9-11).

In addition to the Central Asian finds, Triassic Hymenoptera have been encountered only in Australia, where a remain of Archexyela crosbyi Riel that is very close to our Archexyelinae, was recorded at a site of a similar age (Late Triassic in the state of Queensland). This is additional evidence of the unity of the entomofaunae in Eurasia and Gondwana in the latter half of the Triassic, which has also been noted for the orthopteroids (Sharov, 1969), beetles (Ponomarenko, 1969) and caddis-flies (Sukacheva, 1973). It should only be kept in mind that the Madygen suite from which the insects have been derived

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* Data on the Mesozoic Hymenoptera are summarized in the works by Rasnitsyn (1969, 1975a, 1977b) and Kozlov and Rasnitsyn (1979).

at Dzhyailoucho, was dated until recently as Early Triassic (for more detail regarding the age of this suite see Dobruskin, 1970, 1974; and Ponomarenko and Rasnitsyn, 1974).

As may have been anticipated, the percentage of archaic Hymenoptera in the entomofauna was very small. At Dzhyailoucho their remains amount to about 0.4% of the total number of insect remains (table 4); this is a rough estimate and the figure obtained is not directly comparable with analogous data on other localities. The reason for this is the state of the assortment of remains at Dzhyailoucho. Remains from a great number of interlayers distinctly exhibit signs of having been transported and sorted by the current, i.e. the effect of factors which markedly distort the original composition of the taphocoenosis increasing out of proportion the percentage of the tough remains capable of resisting the damage (such as the wing-cases of beetles, leafhoppers and cockroaches).

It should also be noted that remains of aquatic insects have been excluded from all the estimates of the relative abundance of Hymenoptera, since the size of their populations is determined by entirely different taphonomic laws from those governing the abundance of terrestrial insects, and it is impossible to analyze the two groups together. p.144

TABLE 4

The percentage of Hymenoptera among the impressions of non-aquatic insects

Locality	Age	%	Source	Observations
Dzhyailoucho (Kirgizia)	Middle-Upper Triassic	0.4	Original	
Sogyuty and Kyzyl-Kiya (Kirgizia)	Lower Jurassic	0.6	Original	
Sai Sagul (Kirgizia)	Lower?--Middle Jurassic	0.6	Original	

Table 4 Continued

Locality	Age	%	Source	Observations
Novospasskoe, N. Bryan' (trans-Baykal region)	Lower--Middle Jurassic	2.3	Original	
Uda (trans-Baykal region)	Middle--Upper Jurassic	18*	Original	Tuffaceous sediments
Karatau (Kazakhstan)	Upper Jurassic	2.5	Original	
Zolnhofen (FRG)	Upper Jurassic	18*	Carpenter, 1930	Marine deposits
Baisa (trans-Baykal region)	Lower Cretaceous (Neocomian)	4.5	Original	Fauna from a warmer period
Baisa (trans-Baykal region)	Lower Cretaceous (Neocomian)	5.2	Original	Fauna from colder periods
Bon-Tsagan (MPR)	Lower Cretaceous (Barremian-Aptian?)	2.9	Original	
Unda and Daya (trans-Baykal region)	Lower Cretaceous (Aptian-Albian	0.7	Original	The time of the "Cretaceous revolution"
Kzyl-Zhar (Southern Kazakhstan)	Upper Cretaceous, Turonian	2	Original	
Zerkal'naya (Primor'e)	Paleocene	3.5	Original	
Mo-Clay (Denmark)	Lower Eocene	1.6*	Larsson, 1975	Sediments of an open sea
Green-River (USA)	Middle Eocene	8	Scudder, 1890	
Bambridge Mare (Gr. Britain)	Lower Oligocene	28	Jarzembowski, 1976	
Célas (Southern France)	Lower Oligocene	10	Theobald, 1937	
Brunstatt, Kleinkembs (Northeastern France)	Lower Oligocene	40*	" " " " "	Saliferous deposits
Céreste (France)	Middle Oligocene	3	" " " " "	
Aix-en-Provence (Southern France)	Middle Oligocene	6	" " " " "	

Table 4 Continued

Locality	Age	%	Source	Observations
Florissant (Colorado)	Lower Oligocene	40*	Scudder, 1890	Tuffaceous deposits
B. Svetlovodnaya	Upper Oligocene	30*	Original	Tuffaceous deposits
Granatovaya (Primor'e)	Upper Oligocene--Lower Miocene	10	Original	
Kema (Primor'e)	Lower Miocene	10	Original	
Öningen (FRG) (FGR)	Lower Miocene	20	Scudder, 1890	
Vishnevaya Balka (Stavropol' district)	Middle Miocene	10	Original	
Chon-Tuz (Kirgizia)	Middle-Upper Miocene	8	Original	
Mainz (FRG)	Upper Miocene	14	Zeuner, 1938	
Böttingen (FRG)	Upper Miocene	31*	Zeuner, 1931	Travertites (sediments of hot springs)
Botchi (Primor'e)	Upper Miocene	15*	Original	Tuffaceous sediments
Willershausen (FRG) (FGR)	Upper Pliocene	23	Steinbach, 1967; Gersdorf, 1968	

* Data from localities differing markedly from most of the other localities with regard to taphonomic conditions or paleogeography.

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From the ecological viewpoint the archaic fauna of Hymenoptera was composed entirely of phytophagous forms which probably developed inside the cones of gymnospermous plants.

Liassic

So far the Early Jurassic Hymenoptera have been identified with confidence only at two Lower Liassic localities in Central Asia (Kyzyl-Kiya in Fergana and Sogyuty on the lake

Issyk-Kul'), where we found only three remains: Liadoxyela praecox Mart. at the former site and Kirghizoxyela miribilis A.Rasn. and Sogutia liassica A.Rasn. at the latter. The two first forms belong to the nominal subfamily Xyelidae (sic) (the Liadoxyelini tribe), and the last form has been tentatively referred to the family Xyelydidae (Siricomorpha, Pamphilioidea) that is characteristic of the Late Jurassic, but may belong in reality to a separate group that might be close to the ancestors of the other Siricomorpha. Nor can it be ruled out that Sogutia belongs to Xyelidae Madygellinae. p.145

The hymenopteran fauna thus altered very markedly by the beginning of the Jurassic. There appeared (or perhaps merely increased sharply in abundance) groups of lower Hymenoptera that are more advanced than Archexyelinae and belong at least to another subfamily (Xyelinae); one of their forms may even belong to another infraorder (Symphyta). The Liassic Hymenoptera have so far been little studied and it remains unclear whether Archexyelinae became extinct by the beginning of the Liassic (Madygellinae definitely persisted until the Early Cretaceous) and if not, to what extent did their abundance decrease. The meager store of the material available also makes it impossible for us to judge whether the percentage of Hymenopera in the entomofauna increased by the beginning of the Liassic (the figure obtained for Sogyuta and Kyzyl-Kiya is 0.6%, but it is not very reliable) and whether new ecological types appeared among them (the data available on Sogutia do not include information on its mode of existence).

Jurassic faunae of undetermined age

Several local faunae date back to the time interval between the beginning of the Early Jurassic (Sogyuty, Kyzyl-Kiya) and the Late Jurassic (Katatau, Zolnhofen). Their age has been determined as Middle Jurassic (Sai Sagul in Fergana, Novospasskoe and Novaya Bryan' in the trans-Baykal region, and, farther on, Iya

in the sub-Baykal region, which is roughly synchronous with the famous Ust'-Baley and can therefore scarcely be younger than the very beginning of the Middle Jurassic; probably also Beibyao* in eastern China) or Middle-Late Jurassic (Uda in the trans-Baykal region). The fauna of Hymenoptera is divided into two groups on the basis of their geographic distribution rather than by the probable differences in their age. The Central Asian (Sai Sagul) fauna is most markedly segregated. Its most striking characteristic is the total or nearly complete absence of Xyelidae (the only specimen which may belong to that family is a fragment of thorax which resembles in shape and sculpture the thorax of Archexyelinae, but cannot be identified with greater precision). Xyelididae, including forms resembling Sogutia (undescribed so far), and Siricoidea predominate in this fauna. Among the Siricoidea there have been described representatives of the families Gigasiricidae, Sepulcidae and Myrmiciidae. The forms that have not been described as yet include representatives of the family Pararchexyelidae that is also known from the Late Jurassic and may belong to Siricoidea. In addition to Siricomorpha there has been identified a wing of an extremely archaic and primitive representative of the Apocrita (Proapocritus praecursor A.Rasn., Karatavitidae).

The similarity between this and the Early Liassic faunae is thus negligible even on the level of infraorders (Sogutia is the only link between them).

The decline of the relative abundance of Xyelidae in Sagul versus their percentage in the Early Liassic fauna may reflect the evolutionary tendencies rather than the effect of the climate on the composition of the fauna. As may be seen from the further account, from the time-interval discussed (which we shall tentatively designate as the Middle Jurassic) and at least until the beginning of the Cretaceous, Xyelidae were represented by significant numbers in the faunae of the temperate Siberian floral realm (Vakhrameev et al., 1970), but were relatively few

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* Transliteration. Translator.

in the warmer Indo-European realm regarded as tropical. The distribution pattern of Xyelidae in different strata at Bais Baisa (the Neocomian of the trans-Baykal region, see farther on) corroborates the view that it is a function of the climate. It is also supported by the present-day distribution of this family: Xyelidae are most characteristic of the temperate zone of the Holarctic realm and do not penetrate into the tropical regions. Since both Dzhyailoucho and the Lower Liassic sites are located in the Indo-European realm, have roughly the same position in relation to its boundaries as Sagul, and exhibit no signs of a colder climate, the most logical explanation of the decline in the abundance of an archaic group such as Xyelidae is that they were supplanted by their recently evolved descendants Siricomorpha. The redistribution of the abundance of different groups of Symphyta occurs against the background of the percentage of Hymenoptera in the terrestrial entomofauna remaining as low as it was during the Liassic (table 4). This evidences that Xyelidae were, indeed, p.146
supplanted and decreased in abundance not only in relative, but also in absolute terms.

The similarity between the Sagula fauna and more recent faunae, especially the Late Jurassic fauna of Karatau that is close to it from the climatic viewpoint, is readily perceptible and appears to be greater than its resemblance to the Liassic and, particularly, to the Triassic faunae. The only common element in the faunae from Sagul and Early Liassic faunae is Sogutia and its analogues. On the other hand nearly all the families found at Sagul (Xyelididae, Gigasiricidae, Sepulcidae, Pararchexyelidae and Karatavitidae) are also represented in Karatau or (Myrmiciidae) in the West European localities roughly synchronous with Karatau., such as Zolnhofen or Durdleston Bay in Great Britain. It should, however, be noted that the most abundant Karatau groups (Anaxyelidae and various advanced Apocrita) are lacking in Sagul, while the groups dominant at the latter site play a secondary role in Karatau.

Proceeding with examination of the other localities belonging to this group, we shall start with the fauna of Iya,

Novospasskoe and Novaya Bryan', the most probable age of which is the end of the Early Jurassic or the beginning of the Middle Jurassic.

The most striking feature of this fauna is the predominance of Xyelidae therein (four out of five remains; the forms described are Liadoxyela iensis A.Rasn., Xyelinae Liadoxyelini, Xyelisca leptopoda A.Rasn. and Xyelinae Xyelini), which agrees with the hypothesis associating Xyelidae mainly with temperate climatic conditions.

Secondly, the proportion of Hymenoptera sharply increases in the entomofauna discussed and attains a figure characteristic of the Late Jurassic fauna from Karatau (table 4).

Thirdly, the "Middle Jurassic" fauna from Siberia comprises no endemics of a high taxonomic rank or representatives of groups that are characteristic of older faunae. It only includes groups distributed from the Liassic to the Neocomian (Liadoxyelini), groups persisting even now, but unknown in older faunae (Xyelini), and, lastly, forms that are very close to those found at Karatau. The latter pertains to Cleistogaster buriatica A.Rasn., the second oldest (after Proapocritus A.Rasn.) representative of Apocrita, which belongs to the recent family Megalyridae, but to the same genus as several Karatau species. This fauna is thus close to the Late Jurassic fauna from Karatau and differs from it, similarly to the faunae from the other Mesozoic localities of the Siberian paleofloral realm, only in that it lacks or comprises few xylophagous insects and their parasites.

The Beibyao locality forming part of the same group, was not discussed in the preceding paragraph mainly because it is geographically remote from the Siberian localities, being situated near the southern boundary of the Siberian realm. This may account for the fact that the only hymenopterous insect found there (Paraulacus Ping.) belongs not, as may have been expected, to Xyelidae, but to Apocrita or, more precisely, to Mesoserphidae, the most characteristic family of the Karatau fauna. It may, however, be purely accidental.

Uda differs from the other Siberian localities considerably more markedly in age, which is assumed to be more recent (the end of the Middle Jurassic and the beginning of the Late Jurassic), as well as because of the abnormally high percentage of Hymenoptera in its non-aquatic entomofauna (18%) and a low percentage of Xyelidae (one single remnant out of nine). The relative abundance of Hymenoptera may be due to some so far obscure factors associated with the burial of the insects in tuffaceous sediments, since the other faunae recorded in deposits of that kind (the Oligocene sites Bol'shaya Svetlovodnaya and Botchi in Primor'e and Florissant in the USA) also comprise an unusually high percentage of Hymenoptera. As concerns the low proportion of Xyelidae, the difference between this fauna and the "Middle Jurassic" faunae of Siberia is here clearly evident, but its seemingly obvious resemblance to the fauna from Karatau may be misleading. Given the scantity of the material available, it is impossible to assess realistically the fraction of Xyelidae in this fauna: it may be 6%, as is the case in Karatau, or 17%, as in the relatively thermophilic variant of the fauna from Baisa (the Neocomian of the trans-Baykal region). There are therefore no grounds for sharply separating the Uda fauna from the preceding faunae or for regarding it as a fauna close to that of Karatau. We may even be dealing here simply with a variant of the Siberian fauna that existed under somewhat warmer climatic conditions. This is also suggested by the absence at Uda of xylophagous insects and their parasites (at least of the obvious ones) and by the relatively low percentage of Apocrita (three remains out of nine remains) versus that recorded at Karatau (85%). From the taxonomic viewpoint the fauna from Uda is endoubtedly close to the Karatau fauna: most of the families (Xyelidae, Xyelydidae, Mesoserphidae and Methylonymidae) are found at both sites and are represented by close forms (nearly all of them are species of the same or close genera; Bethylonymus sibiricus A.Rasn., the only species that has already been described, represents precisely the former variant). We have nevertheless no grounds to assume that this similarity is deeper than that between the "Middle Jurassic" Siberian faunae and the fauna from Karatau. The main

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factors distinguishing the Uda fauna from the fauna found at Karatau are the predominance of Xyelydidae in it (three out of nine remains) and the appearance of the earliest Pamphiliidae (Juralyda udensis A.Rasn., Juralydinae). The abundance of Xyelydidae in this fauna appears to be due to the absence of xylophagous Hymenoptera, which constitute the bulk of the fauna at Karatau. Pamphiliidae are found rarely in fossil state and have been encountered only in tuffaceous deposits (in addition to Uda they have been identified only in the Cenozoic deposits at Florissant and Creede in Colorado and at Botchi in Primor'e), so that their absence at Karatau may be related to the taphonomic conditions in that locality.

Attempts to compare the Siberian faunae with the fauna from Sagul on the basis of their similarity to the faunae identified with confidence as Late Jurassic, in particular to the Karatau fauna meet with certain difficulties. The assortment of the families is similar in the two cases, but the proportion of these families varies markedly in different faunae. At a lower taxonomic level the Hymenoptera of the Siberian paleofloral realm are considerably closer to the Hymenoptera from Karatau than to those from Sagul because of the presence of common or close genera. This difference is intensified further if we focus only on the characters that may reflect the evolution of the faunae rather than on the geographic, ecological, etc., variations in their composition, since nearly all the distinctive aspects of the Siberian faunae may be explained precisely by the latter factors. Given the present state of our knowledge of the palaeoecological conditions at Sagul, we cannot do it with regard to that locality. Moreover, because of the absence in the fauna from Sagul of the advanced Apocrita that are found in the Siberian realm, this fauna produces a definite impression of great antiquity. Without pretending to be able to assess the relative age of the two groups of fauna examined here, we are nevertheless compelled to conclude that Sagul clearly reflects the stage in the formation of the hymenopteran fauna antedating the Karatau stage, whereas the Siberian fauna is rather an ecological-geographic variant of the latter.

Late Jurassic

Hymenoptera are known from the Late Jurassic only in three localities: Karatau in Southern Kazakhstan, Zolnhofen in Bavaria (FRG) and Durdleston Bay in Great Britain. The deposits at Sierra del Montsech in Spain, where there have also been found Hymenoptera, were also regarded until recently as Upper Jurassic, but there is now evidence of their being of the Early Cretaceous age (Zherkhin, 1978).

The Hymenoptera found in the Late Jurassic of Europe (Malm) are extremely monotonous, which may be due to their having been preserved in marine deposits. Several tens of Myrmicium schroeteri (Germ.) remains have been obtained from the lithographic slates at Zol'ngofen that have been intensively worked for a long time, and two of the impressions described from Durdleston Bay are represented by M. heeri Westw. and Formicium brodiei Westw. All the three species belong to the family Mrmiciidae.

The fauna of Hymenoptera from Karatau is considerably richer and more varied. It is the largest and most thoroughly studied Mesozoic fauna of that order (excepting the fauna found in Late Cretaceous resins). All the infraorders and twenty families of Hymenoptera are represented in this fauna (Xyelomorpha: Xyelidae; Tenthredinomorpha: Xyelotomidae; Siricomorpha: Pamphilioidea: Xyelydidae, Parapamphiliidae; Siricoidea: Gigasiricidae, Para_chexyelidae, Anaxyelidae, Sepulcidae, Siricidae; Orussomorpha: Paroryssidae; Stephanomorpha: Karatavitidae, Ephialtitidae; Evaniomorpha: Evanioidea; Praeaulacidae, Anomopterellidae; Ceraphronoidea: Megalyridae; Ichneumonomorpha; Proctotrupoidea: Mesoserphidae, Heloridae; Vespomorpha: Bethylonymoidea: Bethylonymidae; infraordo inc. sed.; Karataidae). Praeaulacidae (18% of remains), p.148
Megalyridae (16%), Ephialtitidae (15%), Mesoserphidae (13%) and Heloridae (10%) predominate in it; even the most massive Symphyta are found in lesser numbers: Anaxyelidae and Xyelidae amount to

8% and 6%* respectively. Bethylonymidae (4.5%), Paroryssidae (3.5%), Xyelotomidae and Xyelydidae (2% each) and Siricidae (1.7%) come to a considerable percentage; the other families are represented by single specimens. All the Hymenoptera taken together amount to 2.5% of the total insect number (not counting the aquatic forms). The taxonomic diversity of the Hymenoptera from Karatau clearly distinguishes the Karatau fauna from the Triassic fauna, as well as from the Late Jurassic fauna in Western Europe. The difference in the diversity of the Karatau fauna and of the Jurassic faunae from Siberia is not obvious and may be merely a reflection of the degree to which these faunae have been studied. The collections of Hymenoptera from Karatau are one or two orders larger in volume than those from the other localities of the Triassic, Jurassic and Lower Cretaceous age (with the exception of Bon-Tsaga, the fauna of which has not been studied thoroughly enough as yet). The percentage of Hymenoptera in the collections of insects from Karatau (2.5%) coincides with that recorded for the Jurassic of the Siberian realm, is greater than their percentage at older localities, but lower than that in the Neocomian and Cenozoic (table 4). Among the more recent localities only the entomofauna from Kzyl-Zhar contains a percentage of Hymenoptera comparable to that recorded at Karatau, and their percentage in the Unda-Daya fauna which existed in an anomalous environment (see further on), is considerably smaller. It may therefore be assumed that the Jurassic faunae of Karatau and Siberia occupy an identical and completely natural position in the succession of faunae with a steadily increasing proportion of Hymenoptera.

The distribution of the Karatau families with regard to their abundance is more specific: even though none of the dominant families (representing over 10% of the

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* The distribution described here does not entirely correspond to the figures quoted earlier for Apocrita (Rasnitsyn, 1975a) because erroneous identifications have now been corrected (particularly with respect to Mesoserphidae) and new, hitherto unidentified to the family, finds have been taken here into account.

remains) is endemic of Karatau, none of them attains the same degree of abundance at any of the other localities with a more or less well-studied fauna. On the contrary, the families predominating at those sites (Xyelidae in many Triassic, Jurassic and Early Cretaceous occurrences, Xyelydidae at Sagul and Uda, Myrmiciidae in Jurassic sediments from Europe, and Aculeata in Siberian deposits of the Neocomian age) play here a subordinate role or (the last two groups) are lacking altogether. As concerns the endemic forms of Karatau, their relative abundance is too small to draw any inferences from their absence at other Jurassic localities.

The absence of Myrmiciidae in Karatau may be due to the hot and dry environment in which the Karatau fauna existed (Panfilov, 1968). Myrmiciidae appear to have been associated with hot and humid climates. Their remains have been found in coastal-marine (West European Jurassic) deposits that formed on land, but near a sea coast (the Eocene occurrences of Bournemouth in Great Britain and Wilcox in the USA described by Bennison, Rait*, 1972, and Dilcher, 1973, respectively) or in deposits formed under conditions favourable for the accumulation of coal. The absence of Pamphiliidae from this fauna is probably also due to the hot climatic conditions in Karatau.

The ecological diversity of the Hymenoptera from Karatau appears to include all the main variants represented in the other Jurassic and Triassic faunae, as well as new additional variants. Heloridae that are almost undoubtedly endoparasites, and Bethylonymidae that are probable parasites of beetle larvae with a confined mode of existence, are among the latter. Similarly to many living primitive aculeate insects, Bethylonymidae probably followed the larvae into the substratum (decayed wood, ground cover, etc.) and, having paralyzed the larvae, laid their eggs, and left the larvae there. Furthermore, the fauna of Karatau differs from all the known Mesozoic faunae because of the abundance

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* Transliteration. Translator.

of the parasites of xylophagous insects in it, and it differs from the Triassic and Siberian Jurassic fauna because of the presence and abundance of xylophagous insects (Siricoidea) in it and the small proportion of Xyelidae that inhabited male cones of gymnospermous plants (the latter is also characteristic of Uda). The low abundance of xylophages and their parasites is generally characteristic of the Mesozoic from Siberia (more precisely, of the Jurassic and Neocomian). p.149

It may be inferred from the above discussion that the differences between the Karatau fauna, Jurassic fauna of the Siberian paleofloral realm, and Jurassic fauna of Western Europe are largely due to ecological and geographic factors. The differences with regard to the other faunae (the Triassic fauna, the fauna dated with confidence as Liassic, the fauna from Sagul and the Cretaceous faunae) appear, however, to be mainly of the evolutionary nature.

In conclusion to our survey of Jurassic Hymenoptera we wish to note the specific relationship of this fauna with the subsequent faunae: its discrete character and at the same time its continuity. Indeed, eight of the 21 Jurassic families (Pararchexyelidae, Gigasiricidae, Sepulcidae, Karatavitidae, Praeaulacidae, Amonopterellidae, Bethylonymidae and Karataidae) do not extend beyond the upper boundary of that period, ten cross it in the form of more or less obvious relicts (Xyelotomidae, Xyelydidae, Anaxyelidae, Siricidae, Myrmiciidae, Paroryssidae, Ephialtitidae, Megalyridae and Mesoserphidae), two (Parapamphiliidae and Pamphiliidae) are found in negligibly small numbers in the Jurassic and later fauna, and only Xyelidae and Heloridae are more or less abundantly represented in some types (the former in relatively cryophilic, the latter in more thermophilic) of faunae of the Jurassic and Early Cretaceous age. On the other hand, in spite of the richness of the Jurassic faunae comparable on the level of the species to the diversity of the living faunae (Rasnitsyn, 1969, 1975a), they comprise relatively few "dead-end" groups with the rank of a family, particularly among the higher Hymenoptera. In fact we can refer to them only Parapamphiliidae, Anaxyelidae,

Myrmiciidae and perhaps the little known families Pararchexyelidae and Sepulcidae from among the lower Hymenoptera, and Anomopterellidae and, possibly, Heloridae from among the higher ones. The other families are the "beginners" of groups of the same or higher ranks and while the number of the families crossing the Jurassic-Cretaceous boundary is relatively small, for phylogenetic lines it is rather considerable (see fig. 38).

Chapter 2

Early Cretaceous

Hymenoptera have been found in the Early Cretaceous sediments at a great number of different sites and are distributed at several stratigraphic levels. The Spanish locality Sierra del Montsech (Lower Neocomian, Berriassian-Valanginian, Brenner et al., 1974) occupies the lowest stratigraphic position and the only hymenopteron found there (Ephialtites jurassicus Meunier; Ephialtitidae) belongs to a family characteristic of the Jurassic fauna. Moreover, its presence in the Indo-European paleogeographic realm tallies with the fact that this insect belongs to the ecological group of ylobionts (or, more precisely, is a parasite of xylophagous insects) predominating in the Karatau fauna.

The next stratigraphic level is occupied by Baisa from the trans-Baykal region. The presence of remains of angiospermous plants (Vakhrameev, 1973) and of the insects associated with them (Rasnitsyn, 1969) suggests that this occurrence dates back to the Late Neocomian. The Zaza and Undurga occurrences in the trans-Baykal regions and the Anda-Khuduk occurrence in Mongolia are similar to Baisa with regard to the composition of the faunae found therein and may be close to it in age. Some of the other occurrences poorly characterized by faunal remains may be of the same age or somewhat younger. These localities are discussed below.

Judging from the data available, the trans-Baykal and Mongolian faunae of the "Baisa" type are fairly uniform from the taxonomic and ecological viewpoints. All the species found in the

"minor" localities belong to the same genera as those recorded at Baisa, less often to the genera close to the latter. This assemblage is characterized first of all by a greater percentage of Hymenoptera in the general entomofauna than that in the Jurassic (table 4). Secondly, the fauna obviously has a more advanced aspect. There appear (and in considerable numbers) the first Aulacidae, Ichneumonidae, Proctotrupidae and true Aculeata (Dryinidae, Baissodidae, Pompilidae and Sphecidae). There have also been found here the oldest Pelecinidae and Serphitidae. The absence of many of the families that are characteristic of the Jurassic, is less significant because of the distinctive ecological and geographic nature of this fauna and the inadequate degree to which it has been studied. The total amount of the material collected from the occurrences of this group (65 impressions identified to the level of the family) is almost an order less than that obtained from the one single occurrence at Karatau (477 remains). It is more important that all the groups extending here from the Jurassic are represented by new taxa that are for the most part obviously more advanced and have at least the rank of a subfamily (Siricidae, Anaxyelidae), but more often of a family or even higher (because of the small amount of the material at our disposal we are discussing in fact only the composition of the dominant forms in this fauna). The only exception in this respect are Xyelidae, the composition of which altered relatively little at the Jurassic — Cretaceous boundary. p.150

Prior to analyzing the other characteristics of this fauna, particularly the proportion of different families in it and its ecology, it should be noted that the fauna exhibits a certain lack of uniformity affecting these characters. Many groups of insects (not only Hymenoptera) are distributed unevenly in the Baisa section so that insects of the thermophilic aspect (first of all Orthoptera and large Neuroptera, as well as more primitive cockroaches still furnished with an external ovipositor, archaic Psocoptera and certain other forms) concentrate in its central part (Sukacheva, 1968; Rasnitsyn, 1969; Vishnyakova, 1976; Zherkhin, 1978). This suggests that the deposits in the middle

of the section formed under warmer climatic conditions than those in its upper and bottom parts. The distribution of Hymenoptera is determined to a significant degree by these differences and confirms at least partly their being a function of the climate. Xyelidae that are found in fairly small numbers in the warm indo-European paleofloral realm at least since the Middle Jurassic and clearly gravitate at present towards the temperate Holarctic regions, amount to 80% of Hymenoptera in the extreme parts of the section which are believed to have formed under conditions of a colder climate, but come to a mere 15% in its central parts. Since Xyelidae and other insects characteristic of the extreme parts of the Baisa section (the cockroaches "Mesoblattina" vitimica Vishn., larvae of the beetle Cretotaenia pallida Pronom., and the alder and snake flies Cretochaulius lacustris Pronom.; probably also, but to a lesser degree, a member of the Odonata or Paraneuroptera order Hemeroscopus baissicus Prit.) are absent or rare in other occurrences of this type, it may be assumed that these deposits also formed in a relatively warm environment.

The less thermophilic variant of the hymenopterous fauna includes only Xyelidae, Aculeata and Proctotrupoidea (mainly Proctotrupidae, but also single specimens of Mesoserphidae and Serphitidae). It would be premature to conclude that this fauna had been impoverished until we have more material at our disposal, although the overwhelming predominance of one single group (in this case of Xyelidae) is, indeed, characteristic of impoverished faunae existing in extreme environments.

The predominance of Xyelidae is also interesting in another respect. This is the last fossil fauna on record with a significant proportion of Xyelidae, since later on they disappear almost completely. It would appear that here, too, their relative abundance should be fairly low, whereas in reality it may even be higher than in any of the Jurassic faunae. This is particularly odd since their "partners" in this fauna are largely the most advanced for that time representatives of Hymenoptera, such as Proctotrupidae of a completely modern aspect, Serphitidae and Aculeata (Baissodidae and Pompilidae), while Jurassic relicts

are represented by one single remain of Mesoserphidae. Therefore, in spite of the abundance of Xyelidae in this fauna, it does not look particularly archaic, especially since Xyelidae also include perceptibly advanced forms (Anthoxyela baissensis A.Rasn. belonging to the tribe Macroxyelini associating now exclusively with angiosperms).

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The thermophilic variant of the fauna has a more ordinary aspect. There are no sharply dominant groups in it, as there are not any in Karatau. The five most abundant families (listed in the decreasing order, these are Proctotrupidae, Xyelidae, and Aulacidae, Ichneumonidae and Baissodidae which are on the same level of abundance) comprise about two-thirds of the remains (three-quarters of the remains in Karatau), even though the total number of the families is not exactly small for a fauna known from such a limited amount of material (29 remains). Apart from the families listed above, there have been identified here Sephidae, Siricidae, Anaxyelidae, Ichneumonomimidae, Dryinidae, Sphecidae, as well as a tenthredinoid of an obscure systematic position (Vitimilarva A. Rasn.).

The composition of the two faunal variants furnishes relatively few clues to their ecological range, except perhaps for the abundance in one of them of the relatively cryophilic Xyelidae. Were it not for the scantity of the material available, it would be possible in some cases to reverse the process, i.e. determine the reaction of different groups to the temperature conditions on the basis of their association with a definite type of fauna. Although more than half the families are known only from the thermophilic variant of the fauna, their individual abundance in this fauna is rather small and we have not succeeded in demonstrating that the abundance of any of these families in the more temperate variant is even smaller. The only thing that is fairly probable is the relatively small ecological diversity of the latter variant, particularly its paucity in extoparasitic forms other than Aculeata (among the material at our disposal the remain of Mesoserphidae is their only possible representative). If, however, we examined the two variants of the fauna together, we would,as was mentioned earlier, note first of all their

impoverishment in the forms that lived in wood, and, secondly, the appearance of egg parasites (Serphitidae), of true and varied wasps (including specialized forms such as Dryinidae), and, lastly, of the forms feeding on angiosperms (Mesocephus A.Rasn., Anthoxyela A.Rasn.).

The fauna of Hymenoptera that is next in age, was discovered quite recently in the 1976-1977 collections from the Mongolian locality Bon-Tsagan. So far we have only results from the preliminary identifications of this fauna (in most cases to the level of the family). Hymenoptera are here often similar to those of Baisa, but for the most part are more advanced from the evolutionary viewpoint than the latter. There have also been found here archaic forms close to those described from Karatau, but they are very few in number. The absence of such relicts in the fauna of the Baisa type may therefore be readily explained by the scantity of the material available from this fauna and by the more temperate climatic conditions at Baisa. Data on certain other insects, including stratigraphically important groups, such as Trichoptera, also testify that the deposits of Bon-Tsagan are more recent (the absolute predominance of the shelters of the caddis flies belonging to the form genus Folindusia Vialov; Vyalov and Sukacheva, 1976).

The list of the preliminary identifications of the hymenopterous insects from Bon-Tsagan is as follows: Xyelomorpha: Xyelidae (Xyelinae: Mesoxyela A.Rasn., Spathoxyela A.Rasn., ?Eoxyela A.Rasn.; Madygellinae: ?Xyelula A.Rasn.) - 16 specimens; Tenthredinomorpha: Tenthredinidae genn. -23; Siricomorpha: Xyelydidae (?Mesolyda A.Rasn.) - 1, Parapamphiliidae (?Paramamphilius A.Rasn.) -1; Anaxyelidae (Anaxyelinae, Kempendajinae, and probably two new aberrant subfamilies) - 15; ?Xiphyrdiidae - 2; Siricoidea inc.sed. - 1; Cephidae (Mesocephus A.Rasn.) - 1; Symphyta inc. sed. - 1; Orussomorpha: ?Paroryssidae (a relatively large insect intermediate between Paroryssidae and Orussidae) - 1; Stephanomorpha: Ephialtitidae - 4; Evaniomorpha: Aulacidae (Cretocleistogaster A.Rasn. and other forms of a more typical aspect) - 12; Cretevaniidae (Cretevania A.Rasn.) - 1; Megalyridae (?Leptocleistogaster A.Rasn.)

- 2; Trigonalidae (Trigonalinae) - 3; Stigmaphronidae - 2; Megaspilidae - 2, Ichneumonomimidae (Ichneumonomima A.Rasn.) - 4; Ceraphronoidea inc. sed. - 4; Ichneumonomorpha; Ichneumonidae (for the most part typical forms, only 1 or 2 Tanychorinae) - 24 or 25; Mesoserphidae (resembling more closely the forms found at Uda than those from Karatau) - 3; Heloridae (of the type similar to the Karatau forms with a markedly separated, but very broad first metasomal tergite) - 9; Proctotrupidae - 9; Pelecinidae (?Pelecininae) - 2; Scelionidae - 2; ?Serphitidae (?Serphitinae) - 1; Vespomorpha: Dryinidae (with a more typical venation pattern than that of Baissobius)- 3; Chrysididae (Cleptinae?) - 3; Pompilidae (Pompilopterus A.Rasn.) - 7; Sphecidae (diversified, similar to Archisphex Evans, Angarosphex A.Rasn., Cretosphex A. Rasn., etc.; may be members of the same subfamily Angarosphecinae or Ampulininae) - 45; Scoliidae (Proscoliinae or a separate, even more primitive subfamily) - 1; ?Scolioidea indet - 2; Masaridae (? Euparagiinae - wasps with a variety of venation patterns that are not typical of Vespoidea, including Curiosivespa A.Rasn. or a similar genus) - 10; Aculeata inc. sed. - 7; Apocrita inc. sed. - 17; a total of 242. p.152

According to preliminary estimates, Hymenoptera amount here to about 3% of non-aquatic insects, i.e. somewhat less than in Karatau or at Baisa. The five dominant families (Sphecidae, Ichneumonidae, Tenthredinidae, Xyelidae and Anaxyelidae) constitute only about half the fauna, which testifies to its great diversity relative to the faunae of the Baisa or Karatau type.Phylogenetically advanced groups that are unknown in the Baisa faunae and testify with varying degrees of certainty to the younger age of the Bon-Tsagan fauna, include Tenthredinidae, Cretevaniidae, Stigmaphronidae, Megaspilidae, Ichneumonidae (excepting Tanychorinae), Scelionidae, Chrysididae, Scoliidae and Masaridae; Xyphidriidae, Trigonalidae and Pelecininae may also be referred to these groups, but with a lesser degree of confidence. Among these groups Tenthredinidae and Ichneumonidae alone are abundant enough for their absence from the collections of the Baisa type faunae to be regarded as significant. However, the combined abundance (nearly one-third of all

the remains) and the ecological diversity of all these insects at Bon-Tsagan are so great that it is impossible not to infer that the fauna examined is younger in age. As concerns the Jurassic relicts at Bon-Tsagan (Xyelula, Mesolyda, Parapamphilius, Anaxyelinae, Kempendajinae, Ephialtitidae and Leptocleisteogaster), their combined abundance is one-third that figure (21 impressions versus 75) and their absence from Baisa and its analogues may be simply due to the scantity of the fossil material and, partly, to environmental differences (with regard to xylophilic groups). Nor can it be ruled out that the steadily increasing proportion of relicts in the faunae from the end of the Early Cretaceous (see details farther on) is also responsible to some degree for the composition of the fauna at Bon-Tsagan. The absence of Macroxyelinae among the Hymenoptera from Bon-Tsagan is a highly important criterion for determining the evolutionary level of these Hymenoptera. Macroxyelinae which amount to a large fraction of the Xyelidae remains at Karatau and Baisa, are encountered very rarely in more recent deposits and are represented by very small numbers in the living fauna of that family. The decrease in the total percentage of Xyelidae (from 15% in the thermophilic variant of the Baisa fauna to 7% at Bon-Tsagan) may be due to chronological factors (in the Cenozoic their percentage is practically nil), as well as to the southern position of Bon-Tsagan relative to Baisa. The climatic analogy of Bon-Tsagan with Karatau is sustained by the greater proportion of xylophilic Hymenoptera in its fauna than that found at Baisa, although definitely xylophilic forms (Siricoidea, Ephialtitidae and large Aulacidae) are here considerably fewer than at Karatau.

The collections were gathered at Bon-Tsagan layer by layer, the way it was done at Baisa, but the nature of the non-uniformity of that fauna has not been adequately studied as yet. Hymenoptera exhibit here more or less stable links with the rocks enclosing the impressions. Whereas at Baisa the remains of Hymenoptera have been derived from marls, at Bon-Tsagan they are buried in both marls and siltstones interstratified in the section. Moreover, some groups (Siricomorpha, Pompilidae and digging wasps) clearly prefer

marls, while others (Xyelidae, Ephialtitidae, Evaniomorpha and, in particular, Aulacidae, Ichneumonomorpha as a whole, including fairly definitively Ichneumonidae of a typical aspect, Heloridae and Proctotrupidae) gravitate towards marls. Among the groups more or less abundantly represented in the fauna, Tenthredinidae and Masaridae alone display no distinct association with any definite facies. The interpretation of the distribution outlined above is fairly superficial thus far. The probable cyclicity of the faunal variations has not been determined with adequate confidence as yet. The association of Siricomorpha that were characteristic of the Indo-European faunae during the Jurassic, with siltstones and of Xyelidae, a typically Siberian group, with marls may indicate that siltstones formed in an environment favourable for the burial of thermophilic faunae, perhaps simply under warmer climatic conditions. This is contradicted, however, by the discovery that components of the xylophilic fauna other than Siricoidea (Ephialtitidae and Aulacidae) are confined to marls. It would therefore appear that the causes of the differences in the composition of the remains found in marls and siltstones, respectively, are not restricted to differences in the degree to which the original faunae were thermophilic. p.153

The list of the occurrences with Hymenoptera of the Neocomian (or presumably Neocomian) age is not exhausted by those examined above. Among the other localities Tonbridge in Great Britain, where Archisphex crowsoni Evans (Sphecidae) was found, is readily comparable to Baisa and Bon-Tsagan with regard to their assemblages. Tanychorella A.Rasn. (Ichneumonidae), a more advanced form than Tanychora A.Rasn. that is found at Baisa and other occurrences of that group, but is more primitive than most of the Ichneumonidae from Bon-Tsagan, was discovered at Romanovka in the trans-Baykal region. There are certain other data evidencing the distinctive nature of this occurrence and its presumably somewhat younger age than that of Baisa (Zherikhin, 1978).

Sinosirex giganteus Hong (Hong, 1975), a form belonging probably to more advanced Siricidae than those recorded in Karatau and Baisa (in Bon-Tsagan there are no analogues of Sinosirex), was

found at Naitszykhangou* in the province of Khebei* in China. The exact age of this find is unknown, but it probably is not older than the insects from Bon-Tsagan. The fact that the only representative of Hymenoptera found there is a xylophagous insect may be purely accidental or may be due to one of the following factors: a) The boundary of the abundance of xylobionts passed during the Neocomian somewhere between Bon-Tsagan and Naitszykhangou; b) The fauna at Naitszykhangon is younger than the Neocomian fauna and may not be subject to the laws governing more ancient faunae.

The find of Kempendaja A.Rasn. in Kempendyai (Yakutia) poses a more complex problem. This insect is a siricoid of the family Anaxyelidae and forms a separate subfamily therein. This is the most primitive subfamily of Anaxyelidae in a number of characters. Other as yet undescribed representatives of this subfamily have been found in Bon-Tsagan. The occurrence has been referred to the Neocomian (Korchagin, 1972; Rozhdestvenskii, 1974), but xylophilic insects are rare in the Neocomian of Siberia, and a find of this kind is rather improbable. We are therefore compelled to choose between a fairly improbable accident and the hypothesis that Kempedaja is of the post-Neocomian age and that after the Neocomian xylophilic insects were no longer rigidly confined to the warm climate.

The fauna enclosed in Lebanese resins (the Dzhezin* occurrence) is commonly referred to the Neocomian, but there is also evidence suggesting that it is of a younger (Aptian) age (Zherkhin, 1978). The taxonomic position of the hymenopterous insects from Dzhezin is unknown.

The last part of the Early Cretaceous (the Aptian and Albian ages) is a critical period in the evolution of the continental biota, the time of the "Cretaceous biocoenotic revolution". Mesophytic biocoenoses were replaced during that time by cenophytic biocenoses, in which angiospermous plants and other organisms

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* Transliteration. Translator.

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characteristic of the Cenozoic predominated (Rohdendorf, Zherikhin, 1974; Zherikhin, 1978).

Unfortunately, at the only accurately dated occurrence of Aptian-Albian Hymenoptera (the Khetana river in the Khabarovsk region, Middle Albian) there has been found one single remain belonging to Xyelidae Macroxyelinae. This insect resembles most closely Anthoxyela A.Rasn., a representative of Macroxyelini, but in addition to the attributes characteristic of the latter, it also has characters of two other tribes (Ceroxyelini and Gigantoxyelini). It is rather difficult to assess the evolutionary level of this find, and it therefore contributes nothing essentially new to our understanding of the Aptian-Albian biocoenotic succession. The situation is entirely different at the trans-Baykal occurrences Unda and Daya. Even though the age of these occurrences is debatable, the mixture of advanced groups with relicts that has also been observed in other faunae from the end of the Early Cretaceous, is here particularly striking (Zherkhin, 1978). This is also manifest among the Hymenoptera, but not as clearly as it seemed to us earlier (Rasnitsyn, 1975a). The two hymenopterous insects found here (Undatoma dahurica A.Rasn. in Unda and Cleistogaster dahurica A.Rasn., Megalyridae, in Daya) belong p.154 to groups (a family and a subfamily, respectively) known only from the Jurassic. Moreover, the former is more primitive in some of its characters than Jurassic Xyelotomidae. It is highly probable, but not indisputable that both species are relicts, since the peak of distribution of their respective groups is separated from these finds only by the Neocomian (in other cases the hiatus may also include the major part of the Jurassic and sometimes even the Triassic). Another significant fact regarding Cleistogaster is the presence in the Late Neocomian or Aptian from Bon-Tsagan of Leptocleistogaster, a close genus only slightly more advanced than Cleistogaster.

Admittedly, Cleistogastrinae are very rare in these deposits and their presence there may be due to the same factors as in Daya. In addition to the three occurrences listed above, there are several others that may also date back to the Late Albian, but it cannot be

ruled out that they are actually of the Late Cretaceous (Cenomanian) age. We are referring to the occurrences of fossil resins in Taimyr enclosing a fauna close to that of the resins dated with confidence as Late Cretaceous. This fauna is examined in the next chapter.

Chapter 3

Late Cretaceous

The Late Cretaceous faunae of Hymenoptera are distinctly differentiated into two assemblages differing in taphonomy rather than age. One of the assemblages comprises the faunae of fossil resins enclosing small insects (rarely over 2-2.5mm in length), and the other one amalgamates the hymenopterous insects known from impressions in sedimentary rocks; the finds of the latter kind are rather few and are represented as a rule by specimens measuring 5mm or more in length. This important factor and the differences in the geographic position of the respective major localities where the two assemblages are found (the large insects are known mainly from the territory of the warm Indo-European paleofloral realm, and the small ones from the more temperate Siberian or Siberian-Canadian realm) are responsible for the dissimilarity of the Hymenoptera in the two assemblages. Even families common for both assemblages are few and may be abundantly represented in one of the assemblages, but rare in the other.

It is, however, equally easy to find features of similarity between the two assemblages. For example, both include ants that are not known in the Early Cretaceous. But a much more important common characteristic of the two variants of the Late Cretaceous fauna is their resemblance to the Cenozoic fauna on the one hand, and the marked differences between them and the Early Cretaceous fauna (including that of Bon-Tsaga, which is the closest to them) on the other. Even if representatives of the families which played an important part in the Jurassic or Early Cretaceous (i.e. amounted to over 10% remains in either assemblage) are found after the middle of the Cretaceous, they occur

as obvious relicts (the only exceptions in this respect are Tenthredinidae and Sphecidae which amount to 10 and 15%, respectively, of the hymenopterous remains at Bon-Tsagan and are also fairly common in the Cenozoic faunae). On the other hand the families abundantly represented in the Late Cretaceous and Cenozoic faunae are at best rare prior to the middle of the Cretaceous. A significant proportion of the families does not cross that boundary at all: out of the 31 families known from the Late Cretaceous faunae of hymenopterous insects, 18 families have not been detected in the older faunae and only four families became extinct without crossing the Cenozoic boundary (but among the "practically extinct", families, i.e. families that have not been found among the Cenozoic fossils, there are eight of them: Orussidae, Cretevaniidae, Maimetshidae, Stigmaphronidae, Tetracampidae, Scolebythidae, Falsiformisidae and Masaridae). It is, of course, impossible to assess the magnitude of changes in this simple manner. Of the same number of Early Cretaceous families as that from the Late Cretaceous (32) only seven families (or ten if we include the "practically extinct" families) do not cross the Early-Late Cretaceous boundary. These are Xyelotomidae, Xyelididae, Parapamphiliidae Anaxyelidae, Xiphydriidae, Paroryssidae, Ephialtitidae, Ichneumonomimidae, Mesoserphidae and Baissodidae. Since eight of the 21 Jurassic p.155 families of Hymenoptera do not extend into the Cretaceous, twenty of the thirty-two Early Cretaceous families have not been found in the Jurassic, and twenty of the fifty or so Paleogene (Early Cenozoic) families have not been identified in the Mesozoic, all the boundaries turn out to be "asymmetrical", i.e. the number of the families appearing at each particular boundary is considerably greater than the number of the families becoming extinct there (twice to three times greater if we count the "practically extinct" families). This may mean that the younger faunae have been more thoroughly studied,or it may denote a real diversification of the Hymenoptera (an increase in the total number of their families). The former factor is a realistic explanation only with regard to the last boundary, but even there it is not the main factor. If we compare the percentage rather than the number of the families

appearing and disappearing at the same boundary, the ratios obtained are even closer: 1:1.6 for the Jurassic-Cretaceous boundary, 1:1.9 for the Early-Late Cretaceous boundary, and 1:1.8 for the Late Cretaceous-Paleogene boundary.

In assessing the magnitude of the changes which occurred at the boundaries compared, we shall use the mean percentages of the families becoming extinct at the given boundary on the one hand, and of the families appearing there on the other, instead of the ratios. These mean figures are 0.5:0.45:0.31, respectively, which indicates that the minimum restructuring of the fauna occurred at the Cretaceous-Paleogene boundary. Admittedly, it should be kept in mind that from the viewpoint of taphonomy the Early and Late Cretaceous faunae differ much more markedly from one another than from the other adjacent faunae, and that the principal Jurassic and Early Cretaceous faunae may be separated by a larger time-interval than that centering around the boundary in the middle of the Cretaceous. Consequently, the magnitude of the differences may in both cases appear to be greater than it is in reality. It nevertheless seems probable that for hymenopterous insects the Mesozoic-Cenozoic boundary (the boundary between the Late Cretaceous and the Paleogene) was less rather than more important than the boundary between the Mesophytic and Cenophytic (Early and Late Cretaceous), as is generally the case with continental biocoenoses (Zherkhin, 1978). The Jurassic-Cretaceous boundary appears, however, to have been even more important for Hymenoptera, at least more important than for most of the other insects. Our earlier comment regarding the possible discrepancy in the time-hiatus between the major faunae at the Jurassic-Cretaceous and intra-Cretaceous boundaries, applies not only to Hymenoptera, yet most insects were very similar during the Late Jurassic and Early Cretaceous (Zherkhin, 1978).

The assemblage of large insects

Nearly all the impressions of hymenopterous insects from the Upper Cretaceous are known from the Kzyl-Zhar occurrence

(Southern Kazakhstan, Turonian). The impressions identified here are mainly those of ants (five species from four genera) belonging to Myrmicidae (Ponerinae) and Formicidae (Sphecomyrminae or Dolichoderinae), and of a genus of social wasps (Masaridae Euparagiinae) represented by two species; almost everyone of these species is known from one single impression. A remain which appears to have belonged to a representative of Mutillidae, comes from Bol'shoi Kas (Western Siberia, Cenomanian-Turonian). In the Late Cretaceous deposits of North and South America (Gunlock in the state of Utah, USA, the age of the deposits within the Late Cretaceous is not indicated, and Palasio* in Uruguay, Senonian, i.e. Turonian-Campanian, see Brown, 1941a, and Frenquelli, 1946) there have apparently been found fossil nests of some aculeate insects (see also Bequaert, Carpenter, 1941; and Brown, 1941b).

The restoration after the Aptian-Albian minimum of the relative abundance of Hymenoptera in this entomofauna nearly to the level of the faunae from Karatau and from the Jurassic in Siberia (table 1), is a fairly logical development. The aspect of this fauna that is unexpected for the Late Cretaceous is the overwhelming predominance of aculeate insects, particularly of ants, at Kzyl-Zhar. It is appropriate, however, to recall here first of all the great abundance of Aculeata even in the Neocomian, particularly at Bon-Tsagan, and, secondly, their absolute predominance (over three-quarters of the remains) in many Cenozoic (particularly Oligocene-Miocene) occurrences and their profusion among the living faunae from regions with a hot or warm and dry climate. This is the type of climate presumed for the Turonian in Southern Kazakhstan (the mean temperatures of the warmest and of the coldest months +24 and +22, respectively, and the annual amount of precipitation 500-800mm; Sinitsyn, 1966) and it corresponds approximately to the climate of the savannahs. The subordinate position of Aculeata in the faunae from Late Cretaceous resins may be a result of a different terrain and different climatic conditions (forests with the following climatic parameters for

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* Transliteration. Translator.

the Senonian in Taimyr: the mean monthly temperature interval +17, +12, precipitation 1200-1500mm, Sinitsyn, 1966; judging from these figures, the climate was somewhat similar to that of the coast of California in the USA, but possibly with the polar night!). Furthermore, during the Late Cretaceous there may have been relatively few small culeate insects as yet, which would account for the relatively small abundance of this group in the faunae enclosed in the resins.

It should also be kept in mind that the predominance of Aculeata is characteristic only of some of the local assemblages of Macrohymenoptera from the Late Cretaceous.

When this manuscript was already in print, we received a new rich and very interesting fauna with impressions of Hymenoptera in Cenomanian tuffites from the Obeshchayushchii spring (a tributary of the Nil river at the upper reaches of the Arman' river in the Magadan district). Results of the preliminary identification of that collection are presented below. Unfortunately it was too late to use these data in the other chapters of this work.

The total number of the impressions received is 174. Seven (4%) of them belong to Xyelidae: Xyela (Mesoxyela) spp.; we found here for the first time a complete impression with a 8-segmented flagellum of the antenna in contrast to the 9-segmented flagellum of the nominal subgenus. Tenthredinidae are fairly diversified in this collection and are represented by 13 remains (7%), many of which may belong to Selandriinae or to primitive Tenthredininae of the type of Eriocampa. One of the specimens is a representative of Cephidae; the part of its venation that has survived is more or less typical of Cephinae, but its head is not swollen, its abdomen does not seem to be laterally compressed, as is the case in the other Cephidae, and its ovipositor is gently downcurved near the base of its protective case (the tip of the ovipositor has not been preserved). Siricoidea are represented by two remains: one of them is a representative of Xiphydriidae? (the same as at Bon-Tsagan), and the other one seems to be a member of Anaxyelidae Syntexinae with an even more markedly reduced

venation in the distal part of the wing than that of the living form Syntexis Rohw.

Among the higher Hymenoptera the infraorder Evaniomorpha is represented by one single remain of Ichneumonomimidae exhibiting no perceptible differences from the Bon-Tsagan forms. Fifty-four impressions (31%) belong to Ichneumonidae of a typical (recent) aspect, four impressions (2%) belong to Braconidae, three (2%) to Mesoserphidae (that are similar to the forms found at Karatau, but not to those from Uda or Bon-Tsagan), four (2%) to Heloridae (of the same type as those from Bon-Tsagan), two impressions belong to Proctotrupidae, eighteen (10%) to Cynipidae Aulaxini (highly diverse), and twenty-two (13%) belong to other Microhymenoptera, including Diapriidae, Scelionidae and, probably, Chalcidoidea, which we have not been identified with confidence as yet; the presence among this fauna of other groups of Microhymenoptera also cannot be ruled out. Among the aculeate insects nine impressions (5%) belong to Chrysidoidea (including Dryinidae and Bethylidae) and eleven (6%) to Sphecidae. It is premature to discuss the composition of the latter family, but at least some of its forms with strongly developed notaulae are similar to the forms found at Bon-Tsagan. The only scoliid present (Scoliidae ?Proscoliinae) is similar in venation to that from Bon-Tsagan, however, unlike the latter, but similarly to the Cenozoic Scolioidea, it has a massive metasoma. Its legs, unlike the legs of the other scoliids, are not of the digging type (the impression discussed belongs to a female). Ants are abundant, but not predominant, as is the case at Kzyl-Zhar (12 remains, 7%). They are more primitive than any of the ants known thus far, have large measurements (1-2cm, which explains the scantity of ants in the Upper Cretaceous resins: it was probably small ants that were rare), a venation pattern similar to those of Myrmecia and primitive Ponerinae, a thick, weakly sclerotized metasoma and an upcurved ovipositor. The shape of the first tergite resembles most closely that of the female of Falsiformica, but the next segments (as a minimum the second and the third, but probably also the third and the fourth, the fourth and the fifth) are interspaced by fairly shallow, but distinctly

observable constrictions. This pertains to the abdomen of females. The abdomen of males is somewhat better proportioned and is sclerotized; its constrictions are more clearly defined and it may bear a smaller tubercle on the first tergite. The taxonomic position and phylogenetic relationships of these ants should be subject of a special study. We have not succeeded in identifying more precisely the ten remains of Apocrita from this collection. p.157

The fauna from Obeshchayushchii compels us to elaborate further what we said on p.155. The Hymenoptera from the beginning of the Late Cretaceous are obvious successors of the fauna from the end of the Early Cretaceous. This is particularly clearly evident from the endemic forms of the Cretaceous faunae: Mesoxyela, ?Xyphydriidae, Ichneumonomimidae, Cretevaniidae, Stigmaphronidae, Masaridae, Euparigiinae, characteristic primitive scoliids and, possibly, also from the similarities in the composition of their Tenthredinidae (the absence of Nematinae) and Sphecidae (the abundance of Ampulicinae or their more primitive relatives). The mass appearance of ants and gall wasps makes, however, this boundary very sharp.

The figures reflecting the number of families on the two sides of the main geochronological boundaries change as follows. Of the twenty-one Jurassic families eight do not extend into the Cretaceous; of the thirty-two Early Cretaceous families twenty have not been found in the earlier deposits and seven others (including the nearly extinct ones) have not been recorded in the later sediments; of the forty Late Cretaceous families eighteen are not known from the earlier sediments and fourteen have not been found in the more recent deposits; of about fifty Paleogene families twenty have not been found in the preceding sediments. The ratios of the average percentage of the families that do not cross these boundaries turn out to be 0.5:0 and 37:0.37.

Microhymenoptera of the Late Cretaceous

By now there has accumulated a fairly vast collection of Hymenoptera from the Late Cretaceous resins (including those of

the Albian-Cenomanian age). On our territory, mainly in Taimyr, there have been collected 600 inclusions and there must be a couple of hundred of those obtained from Canadian sites (the exact figures have not been published so far) which brings the total number of these remains to about a thousand. Admittedly, so far only a few groups have been studied in detail and by no means at all the sites, but nearly all the materials available have been identified to the level of the family. This gives us a relatively complete picture of the fauna. It is equally important that the occurrences are distributed virtually throughout the Late Cretaceous cross-section, excepting only the last two stages (the Maestrichtian and the Danian, the latter one of which is now often referred to the Cenozoic), and that the fauna of its initial (the Late Cenomanian from Agapa in Taimyr) and terminal sediments (the Santonian from Yantardakh*in Taimyr and the Campanian from presumably synchronous deposits at Cedar Lake and Medicine Hat in Canada) is known from a large collection of material. The gaps between them are filled by small collections from Turonian deposits at Vilyui (Timmerdyakh-Khai**) and from Turonian and Coniacian sediments in Alaska (Pagnik***); the Bulun****

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* The Yantardakh resins were dated earlier as Coniacian-Santonian (Zherkhin, Sukacheva, 1973; Rasnitsyn, 1975a), but the character of the section at this site (the smooth transition of the resin-bearing beds without visible breaks to the Upper Santonian fossiliferous strata; observations of the author and A.G. Ponomarenko) permits us to narrow down their age interval.

** A new locality that has not been described in the 1975 survey (Rasnitsyn, 1975a); out of the 48 insect remains found there ten belong to Hymenoptera, including 4 Scelionidae, 4 Braconidae, 1 Diapriidae and 1 Serphitidae Mymarommatinae.

*** Transliteration. Translator.

**** The 1976 collections. Of the 68 insects thirteen are hymenopterous including 4 Tetracampidae (?Baeomorpha), 5 Scelionidae and 4 Serphitidae (3 Serphites and 1 Mymarommatinae).

and Romanikhae occurrences in Taimyr, the age of which has not been determined precisely thus far, may also belong to the same time interval (Turonian-Coniacian). Some of the small occurrences coincide approximately in age with Yantardakh [Isaevskii and Sokolovskii in Taimyr and Magothy in New Jersey, USA; the latter occurrence is commonly regarded as Turonian-Coniacian (see Wilson, Carpenter, Brown, 1967, and Rasnitsyn, 1975a), but Doyle, 1969, convincingly argues in favour of its being of the Late Santonian age]. The other occurrences fill the lower segment of the chronological scale. The finds from several localities in the south of France (Schlüter, 1975*) and from Yukhary Agdzhakend in the trans-Caucasus** have been dated, for example, as Lower Cenomanian; the Bediei, Zhdanikh and Kresty occurrences in Taimyr are placed within the Albian-Cenomanian interval.

The age of the highly interesting new occurrence Baikura- p.158
Neru in Taimyr*** is not clear. The geological data pertaining to this occurrence are so far contradictory, but suggest rather the end of the Late Cretaceous. The infrared spectra of the resins analyzed by S.S. Savkevich (VNIGRI) indicate that the resins are of the type that is characteristic of the Kheta suite in Taimyr

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* The composition of the fauna is incompletely known; the work referred to includes an illustration of a representative of Scelionidae, which M.A. Kozlov believes (personal communication) to be of the same type as those commonly found in the resins from Taimyr (fig. 5). In another work (Schlüter, Kuhne, 1975, fig. 7) there is a drawing of a taxonomically obscure representative of the higher Hymenoptera.

** Out of the total of 100 insect remains six are those of Hymenoptera, including 4 Scelionidae and 1 Megalyridae Cretodinapsini (Rasnitsyn, 1977c). One of the representatives of Scelionidae is much more advanced in some of its characters than the other Cretaceous scelionids. See Aliev (1977) regarding the age of the copal-bearing suite where these insects were found.

*** Collections of 1976: out of the total of 246 insects 54 are Hymenoptera including 2 Aulacidae Kotujellinae, 1 Megaspilidae (gen. aff. Dendrocerus), 1 Ichneumonidae, 1 Braconidae, 4 Diapriidae (2-? 1.smarus), 13 Scelionidae, 16 Serphitidae (7 Serphites, 8 Mymarommatinae, and 1 ?Distylopinae), 1 Cynipidae (Aulacini), 5 Tetracampidae (4 Baeomorpha sp., 1 ? subfam. nov. aff. Baemorphinae), 1 Torymidae, 1 Bethylidae and 6 very primitive Formicoidea inc. fam.

(the Yantardakh occurrence), but has not been found in the Cenomanian or older deposits (personal communication). The data on the entomofauna are inconsistent, since it combines old and young elements. This also applies to Hymenoptera which include on the one hand primitive Kotujellinae of the kind unknown after the Cenomanian, and on the other hand a profusion of Chalcidae and ants (albeit very primitive ones) and scant Scelionidae, but no Stigmaphronidae or Cretevaniidae, etc. This fauna differs markedly in composition from the Yantardakh and Cedar Lake faunae and can scarcely be synchronous with them. The abundance of Hymenoptera (over 20% of the insects) at Baikura testifies rather to the great antiquity of this fauna relative to that from Yantardakh (Turonian-Coniacian), but we cannot rule out that it may be of a considerably younger, i.e. Maestrichian age.

The list of the families in the assemblage of Microhymenoptera from the Late Cretaceous is as follows (the extinct taxa are marked with a cross*). No Symphyta have been found. Apocrita are represented by

Orussomorpha
- Orussidae (+Mesorussinae)
- Evanioidea: Aulacidae(+Kotujellinae), +Cretevaniidae
- Ceraphronoidea: Megalyridae (+Cretodinapsini), +Maimetshidae, +Stigmaphronidae, Megaspilidae, Trigonalidae (+Cretogonalinae)

Ichneumonomorpha
- Ichneumonoidea: Ichneumonidae (Tryphoninae), Braconidae (Braconinae, Helconinae, Euphorinae, Microgastrinae).
- Diaprioidea; Austroniidae (Trupochalcidinae), Diapriidae (Ismarinae; subfam. nov.), Scelionidae (Scelioninae s.l.), Serphitidae (+Serphitinae, Mymarommatinae, ?+Distylopinae), Mymaridae** Mymarinae, +Triadomerinae).
- Cynipoidea: Iballidae (Mesocynipinae), Cynipidae (Aulaxini).
- Chalcidoidea**; Trichogrammatinae, Tetracampidae (+Bouceklytinae, Baeomorphinae), Torymidae, Ormyridae,

Vespomorpha
- Chrysidoidea: Bethylidae (Epyrinae, ?Mesitiinae, subfam. indet), Chrysididae (Cleptinae, Amiseginae), Scolebythidae, Dryinidae (Dryininae, subfam. indet).
- Sphecoidea: Sphecidae (Pemphredoninae).
- Scolioidea: +Falsiformicidae (incl. +Taimyrisphex Ev.
- Formicoidea: Formicidae (+Sphecomyrminae), fam. indet

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* In the original text they are marked with asterisks. Translator

** The identifications of the Chalcidoidea and Mymaridae from Taimyr in Rasnitsyn's work (1975a) have been revised by V.A. Tryapitsyn; Baeomorpha sp. has been identified in Agapa; Tetracampidae Baeomorphinae (the dominant group represented by Baeomorpha spp. and gen. aff. Baeomorpha Brues), Torymidae gen. nov. and Ormyridae gen. nov. (both very primitive) as well as Mymaridae Triadomerinae (Triadomerus sp., gen. aff. Triadomerus Yoshimoto) have been found in Yantardakh. The conclusions drawn regarding Baikura-Neru are presented above.

The differences in the composition of asynchronous local faunae may be interpreted in a large measure (but not entirely) as a consequence of evolutionary changes in the Late Cretaceous fauna. The relatively large proportion of extinct families (Stigmaphronidae, Cretevaniidae) in the Cenomanian and Albian-Cenomanian faunae, the increase in the abundance of Serphitinae from the Albian-Cenomanian to the Santonian and the decrease in their percentage towards the Campanian, as well as the gradual decline of the abundance of Scelionidae (up until and during the Cenomian, they amounted to half or more of the total number of Hymenoptera, but in the Santonian this figure dropped to 40% and in the Campanian to about a quarter). In the course of the Late Cretaceous the proportion of Chalcidae increased gradually; they were very rare in the Late Cenomanian, perceptibly present in the Santonian, and fairly numerous during the Campanian. The large number of Chalcididae (four out of thirteen Hymenoptera at Bulun) should not be taken into account, since all of them were found in the same little piece of resin. p.159

The relative abundance of Hymenoptera in the resins from the middle and latter half of the Cretaceous period alters in a regular manner (table 5). If we exclude the fauna of the Lower Cenomanian resins from Agdzhakend, where the low abundance of Hymenoptera (6%) may be due to the differences in the environmental conditions, under which the fauna existed (far southwest from the other occurrences), and some of the local faunae known from a very scant material (fewer than twenty insect remains), we shall see that up until about the middle of the Late Cretaceous, including at least the Turonian, Hymenoptera amount to 20-23% of the insect remains, whereas in the Santonian-Campanian their proportion drops to 13-14%. A close figure (12%) has been obtained for the abundance of Hymenoptera in the Cenozoic (Paleogene) resins from Sakhalin (the exact age of which is not known within the Danian-Eocene interval) and from Arkansas in the USA (Eocene, see Saunders et al., 1974). The data on Baltic amber have not been used, since different authors quote widely varying figures, i.e. 3.4 to 16.5% (see Brues, 1933b; Larsson, 1965; Kelner-Pillaut, 1970);

the spread may be due to the distortions introduced into the composition of the fauna by the use of the standard methods of preparing collections of Baltic amber.

In addition to the local faunae listed above, the highly distinctive fauna from the Burmese resins may also be of the Late Cretaceous age (the alternative, but equally tentative dating of these resins is Paleogene; for greater details see Zherkhin, 1978; Kovalev, 1978). From the viewpoint of the relative proportion of Hymenoptera in this fauna (20%) it belongs to the group of the older Albian-Turonian faunae, but because of the differences in the geographic position and composition of the fauna in question it is risky to use this index as a determining criterion. According to Cockerell (1917a-c, 1920), four of the eight remains of Hymenoptera belong to Bethylidae, three to Aulacidae, and one to Trigonalidae*. There has not been found one single fauna, either living or extinct, where any of these families are at least subdominant. The composition of the other insects in this fauna is also unusual (Zherkhin, 1978).

We shall now attempt a comparison of the Late Cretaceous fauna of Hymenoptera with their fauna from the Cenozoic. This is not a simple task, be it only because the number of the fossil insects described from the Cenozoic is much greater (particularly that of the larger insects, which are also fairly common in Cenozoic resins, unlike their Late Cretaceous counterparts), but far from all of these descriptions are reliable. We could juxtapose only the faunae of Microhymenoptera, but their identifications are particularly often unreliable. Moreover, it is difficult to identify this type of fauna in the Cenozoic, since we cannot simply use the lists of the hymenopterous insects found in the Cenozoic, among which there are also large forms that are not known from

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* The bee Melipkorytes devicus Cock. [=Trigona (Trigonula) devicta (Cock.): Kerr, Maule, 1964] described among the insects found in the Burmese amber (Cockerell, 1921), appears to have been derived in reality from the Anthropogene** copal in Burma (Cockerell, 1922).

** Anthropogene= the Quaternary period plus a portion of the Upper Pliocene. A term introduced by Pavlov in 1922. Translator.

Cretaceous resins. Furthermore, the age interval separating these two faunae is fairly large. The latest more or less reliably dated fauna from the Late Cretaceous resins (in Canada) is of the Campanian age and the first two Cenozoic faunae date back to the Middle (resins from Arkansas in the USA) or Late (Baltic amber) Eocene. These finds are thus separated by the Messtrichtian, Danian, Paleocene and a portion of the Eocene. It cannot be ruled out that the Baikura, Burmese and Sakhalin faunae belong to that interval, but the data pertaining to these p.160
faunae are contradictory and cannot be used at this stage to characterize the time-interval that is of interest to us. The composition of the faunae from Baikura-Neru and from the Burmese amber has already been discussed. The composition of the fauna from the Sakhalin amber (the precise age of which has not been determined within the Danian-Eocene interval) is too distinctive to rule out the effect of some powerful local factors. On the one hand there has been found here Pelecinopteron Tubuliforme Brues, a species described from the Baltic amber (Kozlov, 1974). On the other hand half the Hymenoptera found in this locality are represented by Braconidae Aphidiinae, a phenomenon apparently unheard of anywhere else, with the possible exception of the Middle Oligocene salt-bearing deposits at Wittenheim in Alsace, France (Stary, 1973). Platygastridae are rare in the Paleogene faunae, but amount here to 5% of the hymenopterous insects (more than half the total Microhymenoptera). The composition of the Arkansas fauna is, however, also distinctive (with Mymaridae sharply predominating) and has been inadequately studied (Saunders et al., 1974). Furthermore, the data presented by different authors on the proportion of various groups in the fauna from the Baltic amber (Brues, 1933b; Larsson, 1965) vary widely, which may also be due to the factors mentioned earlier.

TABLE 5

The specific abundance of Hymenoptera in assemblages of insects and in fossil resins

Locality	Age	% of Hymenoptera	Source	Observations
Agdzhakend (trans-Caucasus)	Upper Cretaceous (Lower Cenomanian)	6*	Original	Tropical regions?
Zhdanikha (Taimyr)	The middle of the Cretaceous (Albian-Cenomanian)	19	Original	
N. Agapa (Taimyr)	Upper Cretaceous (Upper Cenomanian)	19	Original	
Timmerdyakh-Khaya (Vilyui)	Upper Cretaceous (Turonian)	20	Original	
Romanikha (Taimyr)	Upper Cretaceous (Turonian-Coniacian?)	20	Original	
Bulun (Taimyr)	Upper Cretaceous (Turonian-Coniacian?)	19	Original	
Yantardakh (Taimyr)	Upper Cretaceous (Santonian)	13	Original	
"Canadian amber"	Upper Cretaceous (Campanian)	14	McAlpine, Martin, 1969; L.Masner(in a letter to the author)	The age has been determined radiometrically (72 million years for each of the two localities with a similar fauna
Baikura-Neru (Taimyr)	Upper Cretaceous (has not been dated more precisely)	22*	Original	
Burmese resins	Upper Cretaceous-Paleogene(has not been dated more precisely)	20*	Cockerel, 1920	Tropical regions
Starodubskoe (Sakhalin)	Paleocene-Eocene	12	Original	
Malvern (Arkansas, USA)	Middle Eocene	12	Saunders et al., 1974	

Table 5 Continued

Locality	Age	% of Hymenoptera	Source	Observations
Baltic amber	Upper Eocene	5.3 8.7	Klebs, 1910 Theobald, 1937	After Kelner-Pillalt, 1970
		6	Ander, 1942	
		3.4 5.1	Brues, 1933b	
		16.5	Larsson, 1965	
Resins from Haiti	Upper Oligocene	50*		
Mizunami (Japan, Honshu)	Middle Pleistocene	25	Hiura, Miyatake, 1974	Tropical regions

* Data on the localities that differ markedly in biogeography from most of the other localities or have not been dated precisely.

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Keeping in mind the data presented above, the results p.161
from the comparative analysis of the Late Cretaceous and Paleogene faunae of hymenopterous insects can be summed up as follows. The proportion of the representatives of that order in the faunae of Microhymenoptera remains the same (see table 5). The variations in the assemblages of large insects are considerable (2% in the Turonian of Kzyl-Shar, 3.5% in the Paleocene from Zerkel'naya in Primor'e; table 4), but first of all, these two faunae are separated by the major part of the Late Cretaceous and, secondly, both have a distinctive composition and existed in markedly different environments. The former fauna is more thermophilic and may also be more xerophilic than many of the other faunae, while the latter one is cryophilic. The rate of extinction of Hymenoptera at the Cretaceous-Cenozoic boundary is relatively low (four out of 32 families).

More definite conclusions can be drawn regarding the changes in the proportion of some groups in the Late Cretaceous and Cenozoic faunae, mainly of those with small body measurements. For example, Scelionidae, which predominated in the Late Cretaceous,

decrease in abundance in the Cenozoic, but remain nevertheless a thriving group. Serphitidae change to relicts in the Cenozoic and their subfamily Serphitinae, which was dominant during the Late Cretaceous, becomes extinct. There appear or greatly increase in abundance Platygastridae, Figitidae and many families of chalcids, and among Braconidae - the subfamilies Aphidiinae and Alysilinae, which are now large; Diapriidae and ants increase in abundance, while the percentage of Bethyloidea diminishes.

Chapter 4

Cenozoic

The situation with the Cenozoic Hymenoptera is rather peculiar. There has accumulated a vast store of material (thousands if not tens of thousands of remains) that has been gathered from a large territory and represents all the ages of the Paleogene and Neogene, but it is difficult to use this material for the analysis of the faunal evolution of Hymenoptera. Many of the faunae were studied a long time ago and on a low level; many others were examined (sometimes even collected) selectively and therefore cannot be used for drawing general inferences with regard to that fauna or for obtaining quantitative data on its composition. The bulk of the material has been derived from the upper half of the Paleogene deposits and from the lower half of the Neogene sediments. This complicates the analysis of the differences between the Late Cretaceous, Paleogene-Neogene and recent faunae. The difficulties involved in this type of analysis were already discussed partly on the preceding pages. The problem is complicated further by our not knowing what the living faunae would look like in the fossil state and how they can be compared with the faunae of the past.

Another factor complicating the study of the Cenozoic hymenopterous faunae is the great diversity of their compositiion. It is greater than that of the Mesozoic faunae and may have arisen as a result of the intensive differentiation of the climate during

the Cenozoic. It requires an extremely detailed analysis of the geographic and local differences in the composition of the faunae, but the data available often prove inadequate for this purpose.

Owing to the circumstances outlined above, at the present stage the studies of the Cenozoic fauna of Hymenoptera are invariably superficial. We therefore examine here this fauna very briefly and mention only its fairly obvious characters. This chapter has been borrowed to a significant extent from V.V. Zherkhin's work (1978).

Even the oldest, i.e. the Early Paleogene faunae differ from the Late Cretaceous faunae in lacking completely extinct families that have not persisted to our days. Myrmiciidae from the Eocene occurrences at Bournemouth in Great Britain and Wilcox in the USA, and Electrotomidae from the Baltic amber of the Eocene age are the only families representatives of which have not been found in younger faunae. The living genera appear to have amounted to roughly half the total number of the genera in the Early-Middle Paleogene. The recent species Fidiobia rugosifrons Crawf. Platygastridae (identified by M.A. Kozlova), p.162 Ambositra famosa Masner (Diapriidae, Masner, 1969) and Palaeo mymar duisburgi (Stein) (Serphitidae, Mymarommatinae, Doutt, 1973) appear for the first time in the Baltic amber from the Eocene (probably from the Late Eocene).

The differences between the Paleocene and later Paleogene faunae are so far unclear, since the only extensive Paleocene fauna at our disposal (Zerkal'naya, Primor'e) existed in relatively cold, possibly mountainous environments and is therefore comparable with difficulty to most of the other faunae. The other known non-thermophilic faunae, such as those from Kema and Granatovaya in Primor'e are much younger than the Tadushinskii* fauna (Upper Oligocene and Oligocene-Miocene boundary deposits). They are distinguished by

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* Transliteration. Translator.

a considerably smaller percentage of Ichneumonidae, which (mainly uniform primitive Pimplinae) amount in Zerkal'naya up to 85% of the Hymenoptera remains, and by the presence of a significant percentage of ants in the fauna from Kema.

Further changes observed in the composition of the Hymenoptera are as follows. In the course of the Eocene and Oligocene the percentage of Ichneumonidae appears to drop. Towards the Late Eocene the abundance and diversity of ants increase sharply. The abundance and diversity of bees increase later, roughly at the Oligocene-Miocene boundary. It is interesting to note that until that time the bees were represented in the Eocene and Oligocene almost exclusively by advanced social forms of the subfamily Apinae. Parasites of higher muscoid flies (Braconidae Alysiinae, Cynipidae Figitinae and Chalcididae) and true gall midges (Platygastridae) begin to flourish at the same time at the Paleogene-Neogene boundary. The changes in the composition of ants are confined to the same boundary: the abundance of Dolichoderinae drops markedly, while that of Myrmediinae increases and the abundance of Formicinae remains high.

A feature characteristic of the Eocene and Oligocene (including tentatively the Early Miocene) is the presence of various Hymenoptera far beyond the boundaries of their present-day range (the fossil material provides so far practically no evidence of the opposite phenomenon, i.e. of their range expanding during the post-Paleogene times). We find it impossible to list here all such instances on record; selected examples are presented below. Blasticotomidae, which do not penetrate at present beyond the boundaries of the Palearctic realm, have been recorded in the Paleocene of North America (Florissant). On the other hand the groups that are now characteristic of the southern (Formicidae Myrmeciinae, Diapriidat Ambositrinae, Megalyridae Dinapsinae, etc.) or western (Pelecinidae) hemisphere, have been found in the fauna from the Baltic and (sometimes) Sakhalin amber. Finds of thermophilic forms are extremely numerous in the occurrences located in the present-day temperate climatic zone, but there is at least one instance of the opposite phenomenon: the genus Palaeomymar

Meun. (Mymarommatinae) does not appear now to penetrate into the tropical regions (we are referring to the tropical zone in its narrow sense, i.e. within the boundaries defined by Razumovskii and Labuntsova, 1969, 1974), but at the end of the Oligocene or at the beginning of the Miocene it existed on the territory which is now part of the tropical zone (it was found in the Mexican amber from the state of Chiapas).

The evolutionary changes in the fauna of Hymenoptera during the Cenozoic are also reflected in its proportion in the entomofauna. The relative abundance of Hymenoptera increases steadily in the faunae known from impressions in the rocks (table 4) between the Triassic and the Neocomian. Towards the end of the Early Cretaceous, at the time of the "Cretaceous biocoenotic revolution", the percentage of Hymenoptera drops sharply, but subsequently rises once again, at least in the course of the Late Cretaceous and Paleogene. It may have continued to grow further, but the data on individual occurrences of the Neogene and, to a lesser degree, of the Oligocene age fluctuate very markedly in a manner that appears to be unrelated to the known taphonomic characteristics of the occurrences in question. In a number of instances the effect of taphonomy is fairly definite, (e.g. the increased percentage of Hymenoptera in the assemblages of insects from tuffaceous sediments and the drop in their percentage in the assemblages from the sediments of the open sea), but we have not succeeded in explaining the spread of the data during the Oligocene and Neogene on the basis of these criteria.

Fossil resins reveal a different picture (table 5): the relative abundance of Hymenoptera declines from the first half of the Late Cretaceous to its latter half, appears to remain p.163
unchanged until the middle of the Eocene and to rise anew at some later point in time. So far we have been unable to determine that moment more accurately because of the scantity of data, as well as because the information pertaining to the Baltic amber is highly contradictory. The reasons for the uncertain nature of the quantitative data were discussed earlier.

It is not particularly surprising that the changes in the specific abundance or the Hymenoptera from the two types of burials follow different patterns. These types of burials differ sharply in taphonomy. Moreover, resins are a highly specific medium from the taphonomic viewpoint (the composition of the fauna enclosed in resins differs more markedly from the original fauna than the fauna found in the form of impressions) and are more stable with regard to their specific characteristics. Therefore, given an adequate amount of data, resins generally provide a clearer picture of the changes in their composition, but reflect the processes which occurred in the original entomofauna, with considerable distortions.

The Cenozoic faunae of Hymenoptera should undoubtedly also reflect the specific geography and local conditions, but in most instances their interpretation is difficult. We can merely note that Tenthredinidae (mainly Nematinae) amount to a relatively high percentage in the faunae believed to have been of a more cryophilic kind: they come to about 20% in Zherkal'naya and Granatovaya in Primor'e, but only to 3-5% or less in the other occurrences. It is interesting to note that these two sites also stand out among the other Cenozoic occurrences (excepting the Paleocene and Early-Middle Eocene ones) on account of the low abundance of ants therein. Nematinae may be regarded as indicators of a relatively cold climate in the Cenozoic, a role performed during most of the Jurassic and in the course of the Neocomian by Xyelidae (at present Nematinae are more characteristic of temperate and, particularly, high latitudes). Further studies should show whether we can regard ants as indicators of a warm environment.

CONCLUSION p.164

The main results of our research can be summed up as follows.

Winged insects arose not later than the latter half of the Early Carboniferous as dendrophilic insects that fed on generative organs of plants. By the Middle Carboniferous the primitive winged insects of the order Protoptera that are referred to the infraclass Scarabaeones, gave rise to the infraclass Gryllones (=Polyneoptera sensu Martynov). Their appearance was a result of the adaptation to the existence in above-ground shelters (concentrations of large plant remains of the type of dead standing wood or "macro-ground cover"). The main evolutionary line of Scarabaeones branched off the Protoptera even earlier, around the beginning of the Namurian. After the divergence of the groups ancestral to Ephemeroptera and Odonata, this line gave rise to the phylogenetically important superorder Caloneuroidea and to its desendants forming the cohort Cimiciformes (Palaeoptera+ Paraneoptera sensu Martynov). Insects with complete metamorphosis (the cohort Scarabaeiformes=Oligoneoptera sensu Martynov), the order Miomoptera, also descended later on from Caloneuroidea (towards the Late Carboniferous). Cimicimorfes, as well as Scarabaeiformes retained initially their association with trees, with the generative organs of the trees in particular. Their evolution involved improvement of flight and of certain other functions. Another feature highly characteristic of Cimiciformes is the optimization of the feeding process through the specialization of the mouth parts altering gradually to a piercing-sucking apparatus. In Scarabaeiformes the most marked changes occurred with respect to their ontogenesis (the separation of the vegetative and morphogenetic functions of the preimaginal period with the appearance of the pupal stage) as a result of their having changed over to developing directly inside the source of food (in strobiles of gymnospermous plants).

The first group of descendants of Miomoptera changed to developing in other substratums (initially probably in the ground

cover, decayed wood, etc.) at the beginning of the Permian or even earlier. The fairly extensive complex of changes related to the new mode of life affected both active stages of development (larva and imago) and led to the appearance of the ancestor of the three related superorders: beetles, Neuropteroidea and Mecopteroidea.

Hymenoptera, another group of the descendants of Miomoptera, branched off considerably later (towards the middle of the Triassic). This process appears to have taken place within the boundaries of the adaptive zone of their ancestors (was not accompanied by readily perceptible changes in ecology) and was associated mainly with the optimization of their adaptations to that zone (first of all the change-over to the dipterous type of flight; the acquisition of haplodiploid mechanism of sex determination may have been a very important development even at the initial stages).

From the moment of its appearance and until the end of the Triassic the order was represented only by its primary group, the family Xyelidae, from which all the other Hymenoptera originated. The information pertaining to the chronological sequence in which the descendants of Xyelidae appeared during the Jurassic, is incomplete because of the scantity of the fossil material and unreliable nature of many datings. The similarity of many Middle and Late Jurassic faunae suggests, however, that the Jurassic fauna evolved mainly during the first half of that period. If this is the case, then all the infraorders of Hymenoptera (including Tenthredinomorpha and Siricomorpha in addition to Xyelormopha among p.165 the lower Hymenoptera, i.e. Symphyta, and Orussomorpha, Stephanomorpha, Evaniomorpha, Ichneumonomorpha and Vespomorpha among the higher Hymenoptera or Apocrita) must have evolved by the middle of the Jurassic (or even by the beginning of the Middle Jurassic). At the same time nearly all the superfamilies (apparently with the exception of Cephoidea) arose among the lower Hymenoptera and all the superfamilies of the first three infraorders (a total of four, since each of the first two comprises one single superfamily), but only a small proportion of the superfamilies from the two last

infraorders, appeared among the higher Hymenoptera.

The evolution of Tenthredinomorpha from Xyelidae (via the subfamily Macroxyelinae and, further on, the family Xyelotomidae) was accompanied by a steadily increasing tendency of the larvae to exist in the open and to feed on leaves, although Tenthredinoidea retained for a long time their primitive mode of life and various groups of these insects moved to the plant surface independently. This trend is weaker among Siricomorpha and has been established only in Pamphilioidea: the break with the generative sphere of the plants and the change-over to their vegetative organs were here probably much more radical. Moreover, the confined mode of existence becomes further accentuated in Siricoidea larvae, which change to the endophytic development inside the plant tissues rather than in the vacant spaces between the plant organs, as was the case with the ancestral groups of Xyelidae. This attribute also persists for a long time among the higher Hymenoptera as well except that their source of food was not the plant, but other insects, initially probably the larvae of Siricoidea.

The higher Hymenoptera appear to have diverged off Siricoidea as part of the common stem with the ancestors of Cephoidea. Their change-over from the xylophagous feeding to parasitism (probably also the concomitant change of Siricoidea from living to dead wood with the ensuing symbiosis of these insects with xylophilic fungi) may have been prompted, for example, by the improvement of the defence mechanisms of the plants against the pests.

The ecological causes of the subsequent stages in the evolution of the higher Hymenoptera remain so far obscure. This applies in particular to the differentiation of the primitive Apocrita into Orussomorpha and Stephanomorpha and to the divergence of the descendants of Stephanomorpha belonging to the infraorders Evaniomorpha and Ichneumonomorpha, since all the four infraorders initially developed on larvae of xylophagous insects (probably Siricoidea) which they infested through the plant tissues with the

help of their ovipositor. A distinct change in the primary mode of existence has been established only for the fifth infraorder, i.e. for Vespomorpha, which also descended from Stephanomorpha. Vespomorpha changed to developing on a different type of hosts (larvae of beetles) inhabiting a less compact substratum (probably decayed wood, perhaps also the ground-cover) and to infesting them by way of a direct contact rather than through the substratum. This involved the ability of the female to penetrate into the substratum, find its victim therein, paralyze it and lay eggs in a confined space. The main prerequisite for these activities was a highly mobile abdomen and, consequently, an ideal abdominal articulation. The tendency to increase the mobility of their abdomen is characteristic of all the higher Hymenoptera, as well as of the Cephoidea that are close to them. Moreover, most representatives of that suborder achieved a considerable amount of success in that direction. The optimal articulation mechanism developed in Vespomorpha, is also characteristic of Ichneumonomorpha and may have been acquired still by their common ancestor. But the assumption that the two infraorders are closely related, remains so far a poorly substantiated hypothesis.

The superfamily Ichneumonoidea is the most primitive ancestral group in the infraorder Ichneumonomorpha. Its appearance during the Jurassic has not been confirmed by paleontological evidence as yet, but is suggested by the existence of Jurassic Proctotrupoidea, which were probably direct descendants of archaic Ichneumonoidea.

Many of the characters of Proctotrupoidea and their descendants (Diaprioidea, Cynipoidea and Chalcidoidea) are causatively related to their small body measurements. This group has been tentatively designated as Microhymenoptera and may have originated from some small (scarcely more than 5-7mm in length) primitive Ichneumonoidea. In addition to a number of distinctive morphological features, most Microhymenoptera (excepting some Chalcidae) are characterized by the endoparasitic development. Endoparasitism is, however, also highly characteristic of many Ichneumonoidea, p.166
particularly of their group that is also distinguished by smaller mean measurements (Braconidae).

As was mentioned earlier, Ichneumonoidea and Proctogrupoidea must have arisen in the Jurassic times. Diaprioidea appeared not later than the Early Cretaceous, and Cynipoidea and Chalcidae evolved in the late Cretaceous.

All the Jurassic Vespomorpha are members of the most primitive superfamily Bethylonymoidea which probably did not have most of the characters found in the aculeate Hymenoptera (Aculeata). The latter include all the Vespomorpha, except for Bethylonymoidea, and are distinguished primarily by the structure of their ovipositor modified to a stinger. Various Aculeata ranging from primitive (Baissodidae) to more advanced forms, such as the superfamilies Pompiloidea and Sphecoidea that are close to Baissodidae, the presumably more distant Scolioidea and Vespoidea, and the markedly segregated Chrysidoidea (=Bethyloidea), arose during the Early Cretaceous. Ants (Formicoidea) probably appeared only in the Late Cretaceous.

From the faunal aspect the history of Hymenoptera may be divided into several stages. The initial stage encompasses the latter half of the Triassic and is characterized by the presence of the only family Xyelidae, among which the archaic subfamily Archexyelinae predominates. The fauna appears to have been homogeneous at that time over an enormous territory (from Angaraland to Australia).

The Jurassic may be characterized as the stage of the incipient evolution (the beginning of the period) and of the relatively stable existence (the end of the period) of the Mesozoic fauna of Hymenoptera as such. The correlation of the two parts of this stage is not clear; the fauna may have arisen and evolved within a relatively short period of time. Jurassic faunae differ markedly from the subsequent faunae in taxonomy, but are closely linked to them by the phylogenetic succession. The taxonomic diversity of the local Jurassic faunae is already comparable to that of the recent faunae, but the ecological spectrum was relatively poor in the Jurassic (its dominant forms were phytophagous insects leading a sheltered existence, and ectoparasites). Jurassic Hymenoptera are known only from Eurasia, and their faunae on that territory were

differentiated ecologically (xylobionts predominated in the west, but were virtually absent in the east).

The Early Cretaceous may be regarded as a stage transitional between the Jurassic that is typical of the Mesozoic (and Mesophytic), and Cenophytic (Late Cretaceous and Cenozoic) stages. The composition of the fauna appears to have been rapidly changing at that time with emergence of the groups characteristic of the Late Cretaceous. The "dead-end" groups which were rapidly becoming extinct during that time interval, were few, as was also the case in the Jurassic. The ecological spectrum of the order expanded on account of phyllophages, endoparasites (including egg parasites) and wasps. An important event of that time was the appearance of the Hymenoptera associated with angiospermous plants. The ecological differentiation of the western and eastern faunae (or, more precisely, of the western and southern faunae on the one hand, and northeastern faunae on the other) persisted at least during the Neocomian (the first ages of the Early Cretaceous epoch).

The "cretaceous biocoentic revolution" (i.e. the replacement of the Mesozoic biocoenoses by biocoenoses in which angiosperms predominated) occurred at the end of the epoch during the Aptian and/or Albian stages. During that time many groups of Hymenoptera became extinct, but some of them, including Jurassic relicts, sharply increased in abundance for a short period of time.

The fauna that is essentially typical of the Cenozoic, arose around the middle of the Cretaceous period (the Cenophytic stage of evolution began). There appeared many groups which also play an important part in later biocoenoses, including the recent ones. From the ecological viewpoint the most important event of that time is the appearance of social Hymenoptera, i.e. of ants. It is interesting to note that other social insects, e.g. termites, appeared at the same time. The pathways along which the sociality of ants developed, differ markedly not only from those of termites, but also from those of the other Hymenoptera.

The Cenophytic stage may be subdivided into several stages of a lower rank. Extinction of the taxa on the level of families (including those which arose during or after the "Cretaceous

revolution") was completed in the course of the initial (Late Cretaceous) period and the fauna increased in diversity. Late p.167
Cretaceous faunae are also characterized by a continuous replacement of dominants and, particularly, of subdominants in successive faunal assemblages (this stage was essentially a period of constant changes). The second, i.e. the Early Paleogene period encompassing the Paleocene and most of the Eocene, is distinguished by a relatively low abundance of Scelionidae, Serphitidae and ants; the last known cases of the extinction of families date back to the Eocene. The Late Paleogene period (from the Late Eocene to approximately the Oligocene-Miocene boundary) is characterized by an abundance of ants, of Formicinae and Bolichoderinae in particular, and by the appearance of social bees. During the Neogene (Miocene-Liocene) Myrmicinae supplanted Dolichoderinae, and solitary bees, as well as parasites of higher (muscoid) flies and gall midgets that were earlier very rare, proliferated.

Geographic differentiation of the faunae is noticeable even in the Late Cretaceous parallel to the existence of the widely distributed, but fairly monotonous fauna of Siberia and Canada. Geographic differentiation of the faunae during the Cenozoic is beyond doubt, but the zoogeographic analysis of Cenozoic Hymenoptera is outside the scope of this work.

Characteristic features of the evolution of Hymenoptera are its continuity, rapidity and non-uniformity, as well as the sensitivity of these insects to changes in their habitat, on account of which they are a promising group as indicators of the age and of the ecological and geographic conditions.

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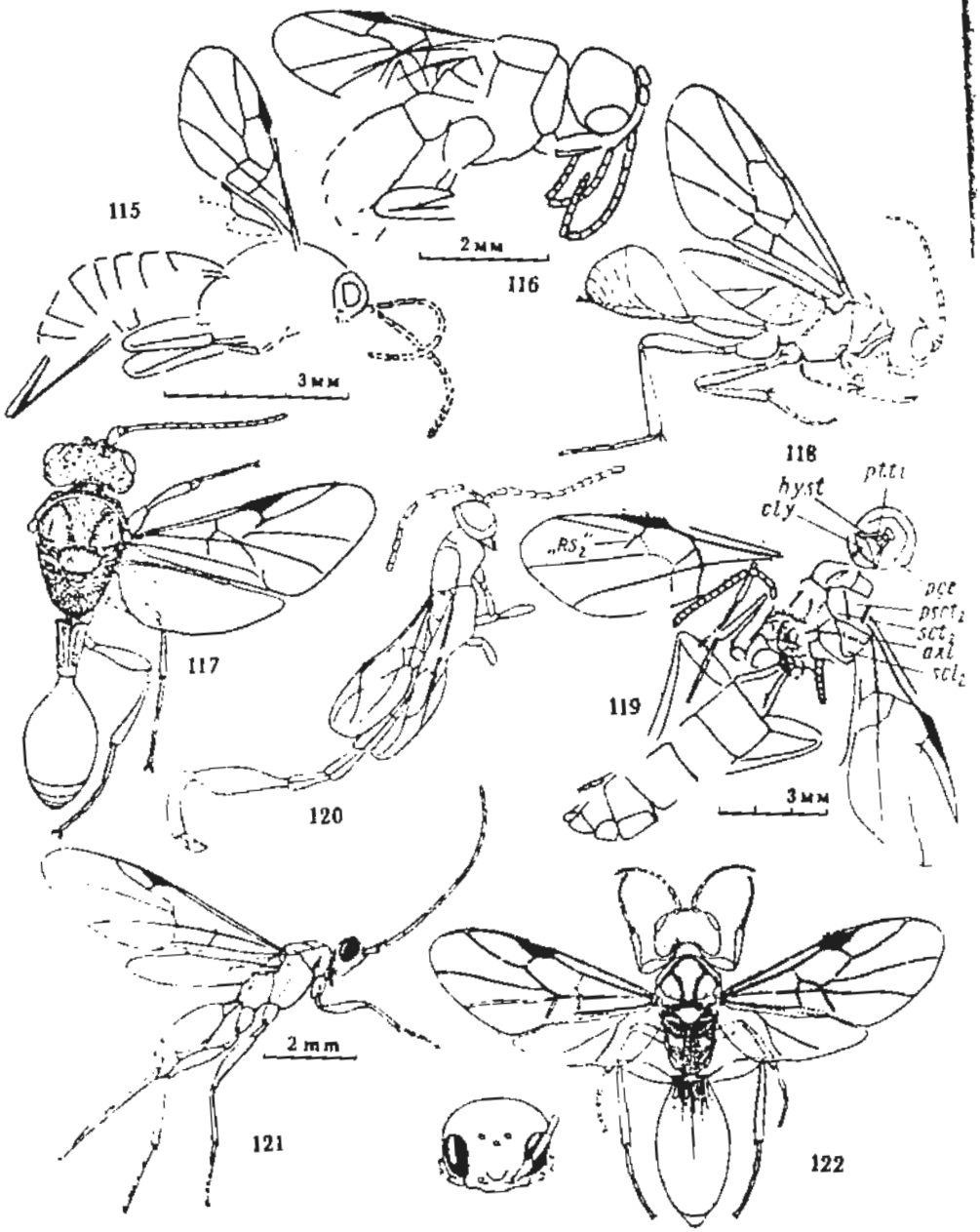
1/4 12. Зак.



Р и с. 115.—122. **Представители надсемейства Proctotrupoidea, семейства Mesoserphidae (115), Heloridae (116—117), Ropronidae (118), Pelecinidae (119—120), Proctotrupidae (121), Vanhorniidae (122)**

115 — Mesoserphus sp., в. юра Южного Казахстана; 116 — Protocyrtus jurassicus Rohd.; в. юра Южного Казахстана; 117 — Helorus rugosus Thoms.; соврем.; 118 — Ropronia garmani Ashm.; соврем.; 119 — Iscopinus baissicus Kozl.; н. мел Забайкалья; 120 — Pelecinopteron tubuliforme Brues; в.олигоцен Прибалтики; 121 — Austroserphus sp.; соврем.; 122 — Vanhornia euchnemidarum Crawf.; соврем. (115, 116, 119 — ориг.: 115 — Каратау, экз. ПИН № 2335/28, 116, 119 — голотип; 117 из Masner, 1957; 118 — из Townes, 1948; 120 — из Козлова, 1974; 121 — из Riek, 1970в; 122 — из Handlirsch, 1925

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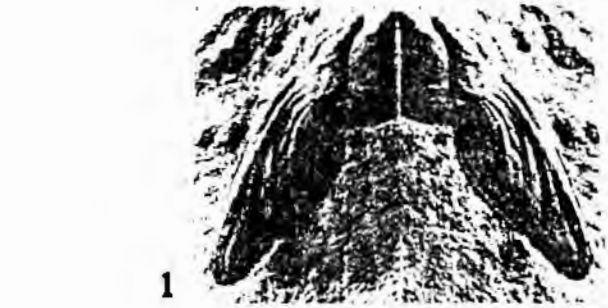
Таблица I



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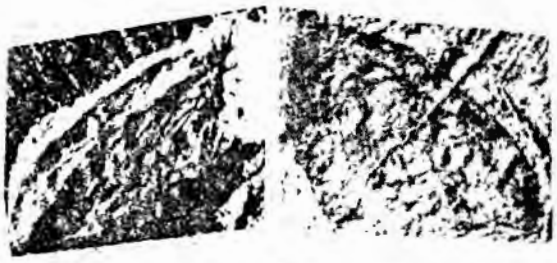

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Таблица II

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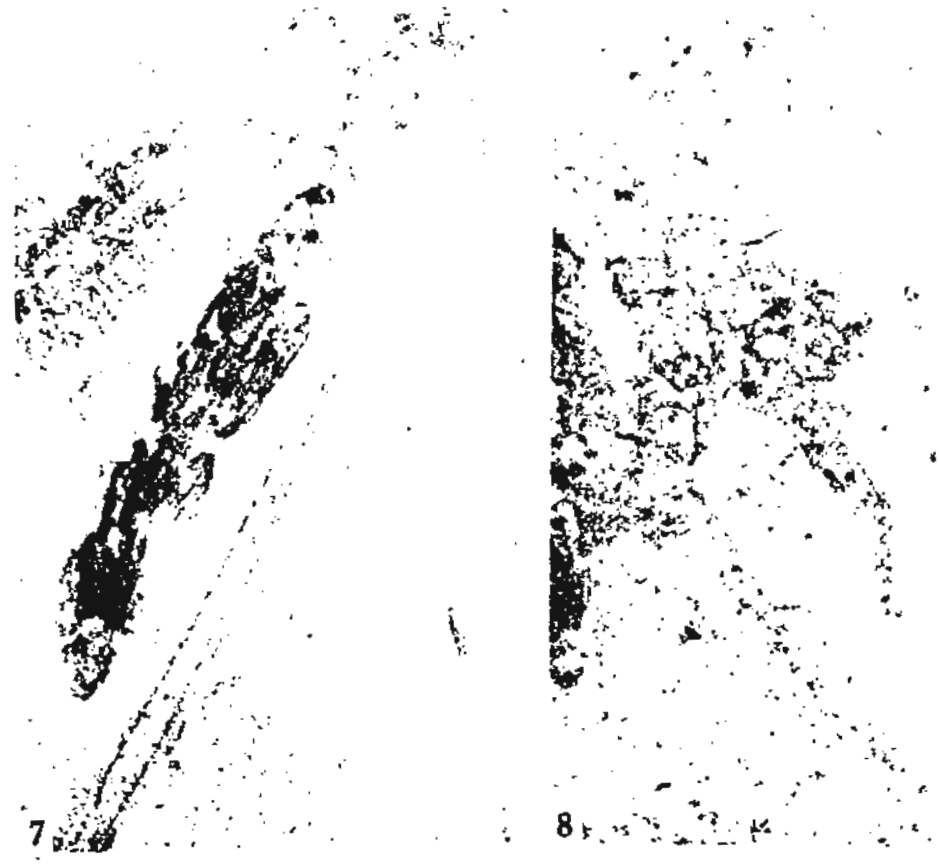

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ОБЪЯСНЕНИЯ К ТАБЛИЦАМ

Таблица I

Нимфальные крылья насекомых из в. карбона Тунгусского бассейна (из Расницына, 1976)

Фиг. 1. Paimbia fenestrata Sin. (из Шарова, 1973), Palaeodictyoptera

Фиг. 2–3. Tchirkovaea guttata G. Zal., Palaeodictyoptera; нимфы двух возрастов

Фиг. 4. Narkemina angustata Mart., Protoblattodea

Фиг. 1 — монтаж нормальной и перевернутой фотографии отпечатка

Фиг. 2–4 — монтаж фотографий прямого и обратного отпечатков

Таблица II

Фиг. 5. Herdina mirificus Carp. et Rich., Ptoloptera; ср. карбон США (из Carpenter, Richardson, 1971) (×4,7)

Фиг. 6. Homoeodictyon elongatum Mart., Hypoperlida?; в. пермь Приуралья; голотип (×1,9)

Таблица III

Фиг. 7. Paleuthygramma tenuicorne Mart., Caloneurodea, н. пермь Приуралья (Чекарда, экз. ПИН № 1700/1424); брюшко самки с яйцами.

Фиг. 8. Голова Marimerobius sp. (Trichoptera), н. пермь Приуралья (Чекарда, экз. ПИН № 212/8) с щупиками, образующими подобие хоботка

Фиг. 9. Участок переднего крыла Mesocynips insignis Cam. (Hymenoptera, Iballidae) с возможным зачатком ареолы

A	— ан
a	— ан
a_1—a_2	— ан
aatg	— со
aem	— ан
aest	— ан
ant	— ан
ap	— ар
astm$_1$	— ан нс тв
atgm$_1$	— ан гс
axl	— ак ср ни
C	— ко
cas	— ш ла
cb	— ба ал
cd	— ка
cdcxm	— ме кс лс
cf	— фу ве то
cly	— на
cnr	— це не
cocc	— за
cpp	— пр
cr	— цв
cratg	— гр
ctd	— ко
Cu	— ку
CuA	— пе
cua	— ку
cu-a	— ку
CuP	— зад
cus	— ку
dg	— ди
dVr$_2$	— ди фе
f	— фу
fant	— ан
fu	— ви
gcx	— го ме
gcxd	— до
gcxv	— ве
gsti	— го бр

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